
THE ANATOMY AND TAXONOMY OF THE
EXQUISITELY PRESERVED GREEN RIVER
FORMATION (EARLY EOCENE) LITHORNITHIDS
(AVES) AND THE RELATIONSHIPS OF
LITHORNITHIDAE

STERLING J. NESBITT AND JULIA A. CLARKE



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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Number 406, 91 pp., 35 figures, 7 tables

Issued June 30, 2016

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ABSTRACT

Fossil remains of Paleogene Palaeognathae are poorly documented and are exceedingly rare. One group of palaeognaths, the lithornithids, is well represented in the Paleogene of North America. Nevertheless, few specimens of the same species are known from each of those Paleogene geologic units. Here, we report five new partial skeletons of lithornithids from the Fossil Butte Member of the Green River Formation (Early Eocene) of Wyoming. One spectacularly preserved specimen is identified as the holotype of a new species, *Calciavis grandei*, gen. et sp. nov., and fully described. Preserved soft tissues (e.g., feathers, pes scales) surround the nearly articulated and complete skeleton. A second well-preserved but disarticulated skeleton is referred to this new taxon. We conclude that there are only two lithornithid taxa in the Green River Formation after careful comparisons with the other known taxon from the same geological unit, *Pseudocrypturus cercanaxius*. Morphological data generated from the new taxon and other Green River Formation lithornithid specimens were integrated into a osteology-only phylogenetic data set containing stem avians as outgroups and extinct and extant members of Palaeognathae (Tinamidae, ratites) and Neognathae (Anseriformes, Galliformes, Neoaves), unnamed lithornithid specimens, and the following named lithornithid taxa: *Lithornis plebius*, *Lithornis promiscuus*, *Lithornis celetius*, *Paracathartes howardae*. We find a monophyletic Lithornithidae (containing *Calciavis grandei*, *Pseudocrypturus cercanaxius*, *Lithornis plebius*, *Lithornis promiscuus*, *Lithornis celetius*, *Paracathartes howardae*) as the sister taxon of Tinamidae at the base of Palaeognathae and also recover a monophyletic Ratitae in the morphology-only analysis. A Lithornithidae-Tinamidae relationship, which could imply a broad Northern Hemisphere distribution in the Paleogene for this total group retracted to the present day Neotropical distribution after the Eocene, is weakly supported in our analysis and is also supported by other lines of evidence such as eggshell morphology. Relationships among flightless palaeognaths and assessment of character homology in this group remain problematic. Indeed, when the morphological analyses were constrained to enforce topologies recovered from all recent analyses of molecular sequence data and retroelement insertions, Lithornithidae is no longer recovered with Tinamidae, which is nested within the now paraphyletic ratites, but remains at the base of Palaeognathae. Thus, regardless of the position of Tinamidae, Lithornithidae is recovered at the base of the clade. However, evidence that many, if not all, of these “ratite” lineages independently evolved similar morphologies related to large size and flight loss suggests that the proposed position of the Lithornithidae remains tentative. Significant morphological variation within Lithornithidae should be captured in inclusive future analyses through use of species terminals.

INTRODUCTION

Palaeognathae Pycraft, 1900, is the sister taxon of all other extant birds (Neognathae) and includes large flightless taxa such as ostriches, moas and elephant birds, as well as the volant Neotropical tinamous. Morphologies ancestral to and relationships within Palaeognathae are important to informing the inference of ancestral conditions for all living birds. From reproductive characters including egg color, palatal and beak morphology, and plumage variation, palaeognaths exhibit morphologies not present in basal neognaths or other Aves. How many of

these morphologies are derived and potentially related to secondary increases in size as well as loss of flight, or may be retained features that inform to the ancestral avian condition has been debated extensively for more than 150 years (Merrem, 1813; Darwin, 1859; Gadow, 1898; Pycraft, 1900; Cracraft, 1974; Cracraft, 2001; Bertelli et al., 2014; Baker et al., 2014; Mitchell et al., 2014). Indeed, the morphology and development of extant (and recently extinct) palaeognaths, as well as their biogeographical distribution on the southern continents, received attention from Richard Owen and Charles Darwin, among many others.

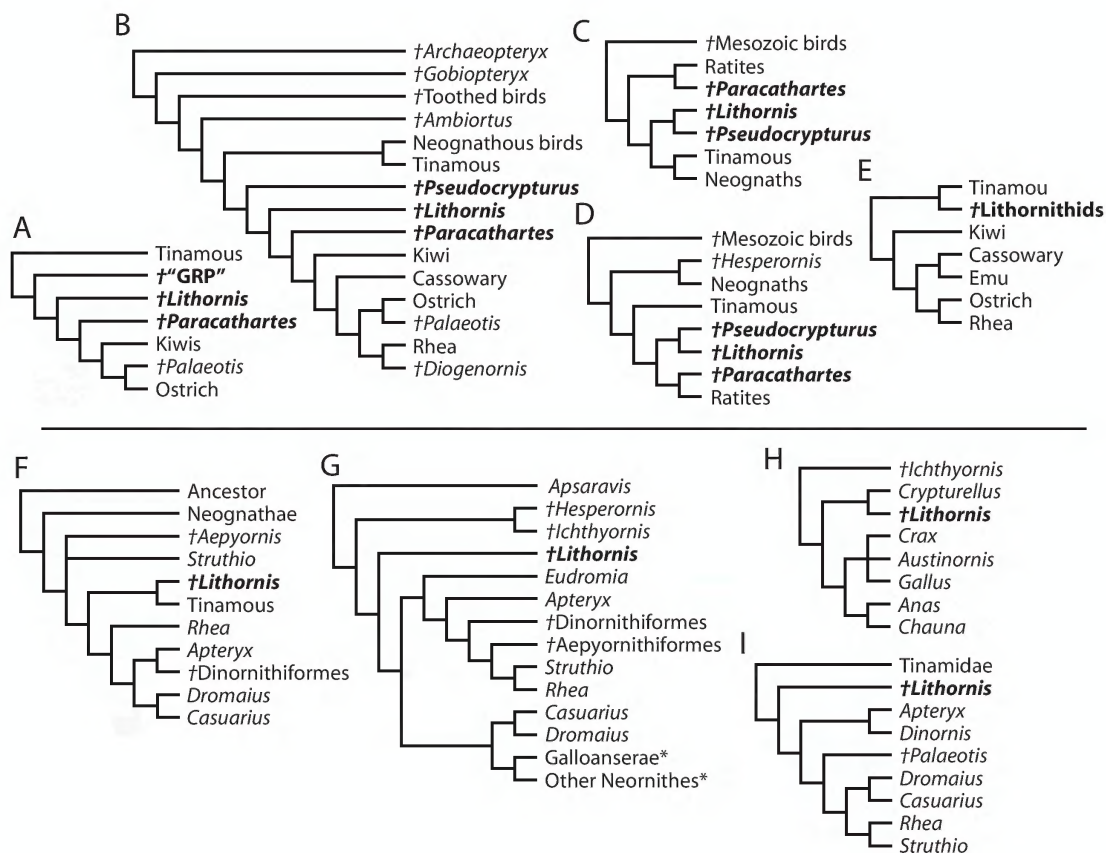


FIG. 1. Previous hypotheses of early diverging avians that incorporated *Lithornis*: **A**, Houde 1986; **B–D**, three alternative hypotheses of relationships proposed by Houde, 1988; **E**, Leonard et al., 2005[§]; **F**, Johnston, 2011; **G**, Livezey and Zusi, 2006; 2007; **H**, Clarke, 2004; and **I**, Dyke, 2003. **A–E** were not based on numerical analyses, whereas the relationships in **F–I** were calculated in phylogenetic programs. Notes: *taxa collapsed into larger clades; † extinct; lithornithids taxa in bold; [§] this position of lithornithids was not found in Dyke, 2003, as cited in Leonard et al., 2005. Abbreviations: "GRP," *Pseudocrypturus cercanaxius*.

Palaeognath taxa such as the recently extinct moas of New Zealand and elephant birds of Madagascar sample extremes in body size, and most palaeognath subclades are secondarily flightless. These flightless forms have been included in a taxon "Ratitae" Merrem, 1813. Only the extant Neotropical tinamous (Tinamidae; ~65 species; Bertelli et al., 2014) are volant. Given conflicting phylogenetic estimates of palaeognath relationships, when and how many times flight was lost is unresolved (Harshman et al., 2008; Phillips et al., 2010; Smith et al., 2013a; Haddrath and Baker, 2012; Baker et al., 2014;

Mitchell et al., 2014). Whether the primarily Southern Hemisphere distribution of extant "ratites" is explained by the Mesozoic breakup of the supercontinent Gondwana (Cracraft 1974; Cracraft, 2001) or, as recent molecular phylogenetic data sets (Harshman et al., 2008; Phillips et al., 2010; Smith et al., 2013a; Haddrath and Baker, 2012; Baker et al., 2014; Mitchell et al., 2014) indicate, more-recent volant dispersal with multiple convergent losses of flight has been debated. Key to fully assessing these alternative scenarios has been the phylogenetic placement of extinct palaeognath taxa (Houde, 1986), in particular

that of the volant Lithornithidae from the early Paleogene of Europe and North America.

Houde and Olson (1981) first argued for the importance of lithornithids to palaeognath relationships with the discovery of a largely complete skull from the Green River Formation and partial skeletons from the other Paleocene deposits of the western United States. Soon after, Houde (1986) incorporated an Eocene Green River palaeognath specimen ("GRP"), *Lithornis*, and a second taxon placed in the genus *Paracathartes* into a phylogeny of palaeognaths, suggesting that these *Lithornis*-like taxa may be paraphyletic with respect to ratites. *Lithornis* and *Lithornis*-like taxa have been included in two types of phylogenetic hypotheses, hand-drawn phylogenies based on character distributions and computer calculated phylogenies (fig. 1). The first analyses were hand-drawn phylogenies based on character distributions (Houde, 1986; 1988). Houde (1988) provided a number of alternative hypotheses with alternative placements of the three *Lithornis*-like taxa, and tinamous. In addition, Houde (1986; 1988) introduced the hypothesis that the *Lithornis*-like taxa and tinamous may represent the plesiomorphic body plan of palaeognaths and thus not necessarily a monophyletic clade. To support this idea, Houde (1988) provided growth evidence from histological sections of the tibiotarsus that indicated that *Paracathartes* grew more like a ratite than the other lithornithids, and *Pseudocrypturus* (= "GRP" of Houde, 1986) uniquely shares posteriorly directed processes on the palatines with kiwis and tinamous. Furthermore, conspicuously like most ratites, lithornithids lack the ossified supratendinal bridge present in tinamous and most other crown-group birds. Indeed, in some optimiza-

tions (Houde, 1988), Palaeognathae was not recovered as monophyletic, but tinamous were placed as more closely related to these other taxa (in Neognathae).

The monophyly of all extant and recently extinct palaeognaths has been supported by all recent phylogenetic analyses (e.g., Cracraft and Clarke, 2001; Livezey and Zusi, 2007; Harshman et al., 2008; Phillips et al., 2010; Smith et al., 2013a; Haddrath and Baker, 2012; Baker et al., 2014; Mitchell et al., 2014), although these relationships have continued to be debated for some time. Subsequent phylogenetic hypotheses of the placement of parts of Lithornithidae were undertaken through analyses focused alternatively on the placement of fossil taxa outside the crown clade or of extant birds (Clarke and Chiappe, 2001; Norell and Clarke, 2001; Clarke and Norell, 2002; Dyke, 2003; Clarke 2004; Livezey and Zusi, 2006; 2007; Johnston, 2011). Extant palaeognath monophyly was recovered in these morphological analyses, whereas the phylogenetic placement of Lithornithidae varies markedly. Clarke and Chiappe (2001) recovered *Lithornis* as the sister taxon to all extant birds based on a limited set of only 72 pectoral characters. Livezey and Zusi (2006, 2007) recover a similar placement, outside of crown Aves, based on more than 1000 morphological characters. By contrast, other analyses including ~200 characters from the whole skeleton and focused on Mesozoic stem-clade avian relationships (e.g., Clarke and Norell, 2002; Clarke, 2004; Clarke et al., 2006), consistently recover *Lithornis* nested within crown Aves as the sister taxon to the only extant palaeognath species exemplar included, a tinamou. Debates over lithornithid affinities mirror debates about the phylogenetic affinities of parts of Palaeo-

FIG. 2. Lithornithids from the Green River Formation of Wyoming. **A**, Holotype skull and cervical vertebrae of *Pseudocrypturus cercanaxius* (USNM 336103) in left lateral view. **B**, WGS U1b-2001, a partial skeleton missing the pectoral girdle, cervical series and skull but bears exquisite feather preservation. **C**, The holotype skeleton of *Calciavis grandei* gen et sp. nov (AMNH 30578). **D**, FMNH PA 739, an articulated skeleton missing the cervical series and much of the skull. **E**, USNM 424078, cast of a nearly complete, articulated skeleton of the privately held Siber and Siber specimen of Houde (1988). **F**, AMNH 30560, a well preserved, partially articulated skeleton missing the pelvic girdle and much of the hind limbs. Scales = 1 cm (**A**); = 5 cm (**B**–**F**).



gnathae more broadly. Morphological and molecular data sets have yielded substantially different phylogenetic arrangements with nearly every possible subclade relationship proposed (e.g., Clarke and Chiappe, 2001; Clarke, 2004; Cracraft, 1974; Bledsoe, 1988; Lee et al., 1997; Dyke, 2003; Livezey and Zusi, 2006, 2007; Harshman et al., 2008; Bourdon et al., 2009; Johnston, 2011; Bertelli et al., 2014; Mitchell et al., 2014).

The name-bearing species of *Lithornis* is *Lithornis vulturinus*, first described from the early Eocene London Clay (Owen, 1840). As further discussed below, the holotype of this specimen was destroyed or lost during World War II and a neotype was identified (Houde, 1988). The purported earliest occurrence of the clade is from the very latest Cretaceous or earliest Paleocene of New Jersey, close to the K/Pg boundary, and this record is supported by the presence of an anterior portion of the scapula with the distinctively recurved acromion, so far autapomorphic of the clade (Parris and Hope, 2000; Hope, 2002; see below). The next-oldest records are of *Fissuravis* from Walbeck, Germany, and *Lithornis* specimens from the Bangtail Quarry and Goler Formation in western North America (Houde, 1988; Mayr, 2007; Stidham et al., 2014). The youngest-known occurrences are from the middle Eocene Bridger Formation (Houde, 1988) and Messel, Germany (Mayr, 2009). European lithornithids range in age from the Selandian–Thanetian (Paleocene; see Stidham et al., 2014) to the early middle Eocene Messel Formation of Germany (Mayr, 2009). All lithornithids described from the Cenozoic are late Paleocene or early middle Eocene in age (Houde, 1988).

The lacustrine Fossil Butte Member of the Green River Formation from Wyoming have yielded much of our knowledge of Paleogene avian diversity in North America, and contain nearly all known avian diversity within the Eocene Green River Formation (Grande, 2013). That member represents extremely well-characterized near-shore and midlake deposits from Fossil Lake, the smallest of the major Green River Formation paleolakes (fig. 2; Grande, 1984, 1994, 2013;

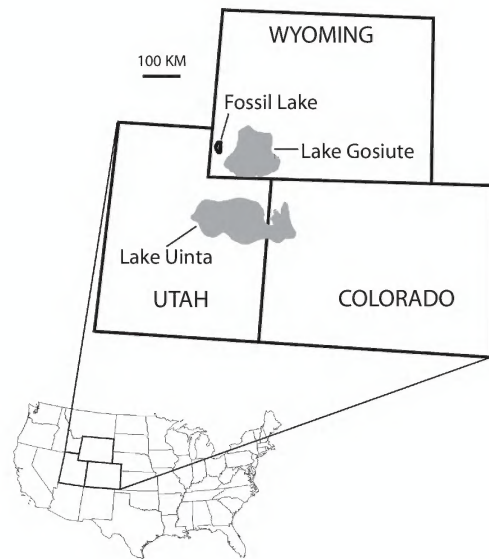


FIG. 3. The lithornithid skeletons emanate from the Fossil Butte Member (Early Eocene) of the Green River Formation of Fossil Lake in Wyoming. Modified from Grande and Buchheim, 1994.

Grande and Buchheim, 1994. The Fossil Butte Member deposits are late early Eocene/earliest middle Eocene in age with an upper bound of 51.66 ± 0.09 Ma (Smith et al., 2008).

Only two lithornithid specimens have so far been described from these deposits (fig. 2). The holotype of *Pseudocyrpturus*, consisting of a skull and partial neck is deposited at USNM, but a referred, nearly complete specimen used in the description of this taxon is in a private collection (Siber and Siber Collection, Switzerland). Here, we provide a description of a new species of lithornithid, utilize five new specimens of lithornithids to provide new details on the osteology and preserved feathering in Lithornithidae, and assess variation observed among the lithornithids from the Green River Formation. Our goals for the phylogenetic analysis were threefold: (1) to assess the Green River Formation lithornithid specimens on a specimen level; (2) to test the monophyly of Lithornithidae; and (3) and to illuminate their phylogenetic relationships within Aves. The

new specimens described here join the approximately 20 described species of birds from the Fossil Butte Member of the Green River Formation (fig. 3) (Eastman, 1900; Brodkorb, 1970; Feduccia and Martin, 1976; Olson, 1977, 1987, 1992; Houde, 1988; Houde and Olson, 1992; Mayr, 2000; Mayr and Daniels, 2001; Mayr and Weidig, 2004; Olson and Matsuoka, 2005; Weidig, 2006, 2010; Ksepka and Clarke, 2010a, 2010b; Ksepka et al., 2013; Smith et al., 2013b). Among large-bodied taxa in the deposits, lithornithids are approximately the third most abundant taxa after the stem frigatebird *Limnofregata* (Olson and Matsuoka, 2005) and the wading anseriform *Presbyornis* (Livezey, 1997), which is abundant in the shoreline deposits surrounding the lake.

The fossils described here also illuminate modes of preservation in Fossil Lake. Lithornithids from the Fossil Butte Member are all known from near-shore deposits (fig. 2), and the partial skeletons we discuss are preserved with and without feathering. The mode of feather preservation in these lithornithid specimens varies. In sites in which the fossil-bearing layers are kerogen rich, with abundant organics, the preserved feathers are conspicuous, and other specimens derived from layers with few visible organics preserve feathers as fine uncolored impressions. A comprehensive study of the taphonomy of the fossil lake birds is outside the scope of the present study. However, we comment on the variation observed within this single taxon, Lithornithidae. The sublocalities within the lake (fig. 3), as well as locality designations follow Grande (2013).

ANATOMICAL ABBREVIATIONS

?	unknown
a.	articulates with
ac	acetabulum
an	angular
ar	acromion
II:1	manual phalanx II:1
cev	cervical vertebrae

cev #	cervical vertebra number
cmc	carpometacarpus
co	coracoid
cp	costal processes
cs	coracoid sulcus
cv	caudal vertebrae
d	dentary
D#	digit number
ec	ectethmoid
ep	extensor process
f	frontal
fe	femur
fi	fibula
fo	fossa
fu	furcula
g	groove
h	humerus
hy	hyoid
if	iliofibularis crest of the ilium
il	ilium
ish	ischium
j	jugal
k	keel
l.	left
la	lacrimal
lc	lateral condyle
m	mandible
mc	metacarpal
mdc	medial condyle
me	mesethmoid
mx	maxilla
n	nasal
p	pit
pa	parietal
pap	papillae
pe	pelvis
pi	pisiform
pmx	premaxilla
po	postorbital process
pop	paroccipital process
pp	pisiform process
pr	primary feather rachis
pt	pterygoid
pu	pubis
py	pygostyle
or	otic region

q	quadrate
r	radius
r.	right
ra	radiale
rb	rib
rc	rachis
rp	retroarticular process
sac	sacrum
sc	scapula
sec	secondaries (feathers)
sk	skull
so	sclerotic ossicle(s)
sp	splénial
sq	squamosal
sr	scar
st	sternum
su	surangular
sv	sacral vertebrae
tbt	tibiotarsus
tmt	tarsometatarsus
tv	thoracic vertebrae
u	ulna
ul	ulnare
un	uncinate process
v	vomer

INSTITUTIONAL ACRONYMS

AMNH	American Museum of Natural History, New York, NY
FMNH	Field Museum of Natural History, Chicago, IL
GM	Geiseltalmuseum, Martin-Luther University, Halle/S., Germany
HLMD	Hessisches Landesmuseum, Darmstadt, Germany
IGM	Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Belgium
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge MA
MGUH	Geologisk Museum of the University of Copenhagen, Dansk Fossil Collection, Copenhagen, Denmark
NHMUK	Natural History Museum, London, UK

PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
PU	Princeton University Collection (now at YPM)
ROM	Royal Ontario Museum, Toronto, Canada
SMM	Sternberg Museum of Natural History, Hays, KS
TMM	Vertebrate Paleontology Laboratory (avian collection), Texas Natural Science Center, Austin, TX
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.
WDC	Wyoming Dinosaur Center, Thermopolis, WY
YPM	Yale Peabody Museum, New Haven, Connecticut

TERMINOLOGY

We follow the principles of systematic taxonomy outlined by de Queiroz and Gauthier (1990) for naming taxa. We use the term *Aves* as a crown-group definition following Gauthier (1986), and the species modifiers of Gauthier and de Queiroz (2001) and the crown-group definitions of *Palaeognathae* Pycraft, 1900, *Neognathae* Merrem, 1813, *Neoaves* Sibley et al., 1988, and *Galloanserae* Sibley et al., 1988, following Gauthier and de Queiroz (2001). However, we do not use *Ratitae* Pycraft, 1900, as a formal clade name as proposed by Gauthier and de Queiroz (2001). Current molecular phylogenies indicate that, as defined by these authors (extant taxa more closely related to *Struthio* than to *Tinamus* or *Vultur*), the name *Ratitae* may apply only to *Struthio* and not any other part of *Palaeognathae* (e.g., Harshman et al., 2008; Haddrath and Baker, 2012; Mitchell et al., 2014). Here the informal name “ratites” refers to extant and extinct large-bodied flightless palaeognaths in keeping with more than 100 years of usage of this informal name. We also recommend that the formal definition of *Tinamidae* Gray, 1840, be revised to include

specifiers of all other major extant and recently extinct palaeognath clades or internal specifiers only. Its current published phylogenetic definition (i.e., all extant taxa more closely related to *Tinamus* than either *Struthio* or *Vultur*; Gauthier and de Queiroz, 2001) in many recent phylogenies would apply the name to a clade that may include all or most other palaeognaths other than *Struthio*. Here, we use the name in this recommended sense to reference only the most recent common ancestor of extant tinamous and all of its descendants. Species conventions follow Dayrat et al. (2008).

Osteological and myological nomenclature follows Baumel and Witmer (1993) and others (Howard, 1929; Clark, 1993; Baumel and Raikow, 1993; Vanden Berge and Zweers, 1993; Clarke, 2004). English equivalents of the Latin osteological nomenclature are used and the Latin equivalent is also given in character states. “Anterior” and “posterior” are used rather than “cranial” (and “rostral” in the skull) and “caudal” as is common in the description of other tetrapods including nonavian dinosaurs.

SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758

(sensu Gauthier and de Queiroz, 2001)

Palaeognathae Pycraft, 1900

(sensu Gauthier and de Queiroz, 2001)

Lithornithidae Houde, 1988

DEFINITION: The most inclusive clade containing *Lithornis promiscuus* Houde, 1988, but not *Apteryx australis* Shaw and Nodder, 1813, *Dromaius novaehollandiae* Latham, 1790, *Dinornis novaezealandiae* Owen, 1843, *Rhea americana* Linnaeus, 1758, *Struthio camelus* Linnaeus, 1758, *Aepyornis maximus* Geoffroy Saint-Hilaire, 1851; *Tetrao (Tinamus) major* Gmelin, 1789, or *Passer domesticus* Linnaeus, 1758.

DIAGNOSIS: Differentiated from other avians by the following unique combination of characters states: broad, flat ventral process of the lacrimal in lateral view (character 13:state 1); quadrate with small fossae on the posterodorsal

portion of the body (C38:1); short fingerlike retroarticular process just posterior to the articular facets of the mandible (C60:1); centrally located ovoid foramina on the lateral surfaces of the centra of the thoracic vertebrae (C67:2); foramina present on the posteroventral surface of the hooked acrocoracoid process of the coracoid (C95:1); acromion of the scapula strongly laterally hooked with small foramina on its posterior surface (C104:2); infratrochlear fossa deeply excavating the proximal surface of the pisiform process on the ventral surface of the carpometacarpus (C136:1); distinct tubercle present on the ventral side of the proximal portion of metacarpal III (C143:1). The Lithornithidae also lack an ossified supratendinal bridge on the tibiotarsus and an enclosed ilioischadic fenestra, possess a concave scapular cotyla, and have an open capital incisure on the humerus. These character states are ambiguously optimized but may serve as an additional differentia (also see Discussion).

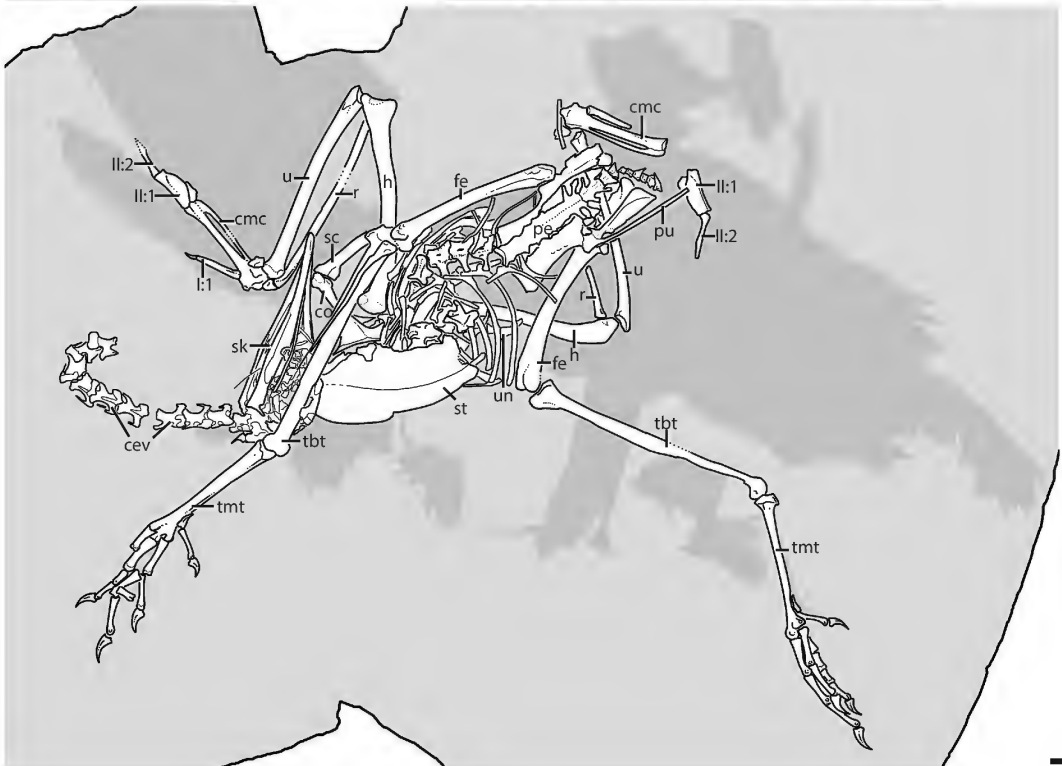
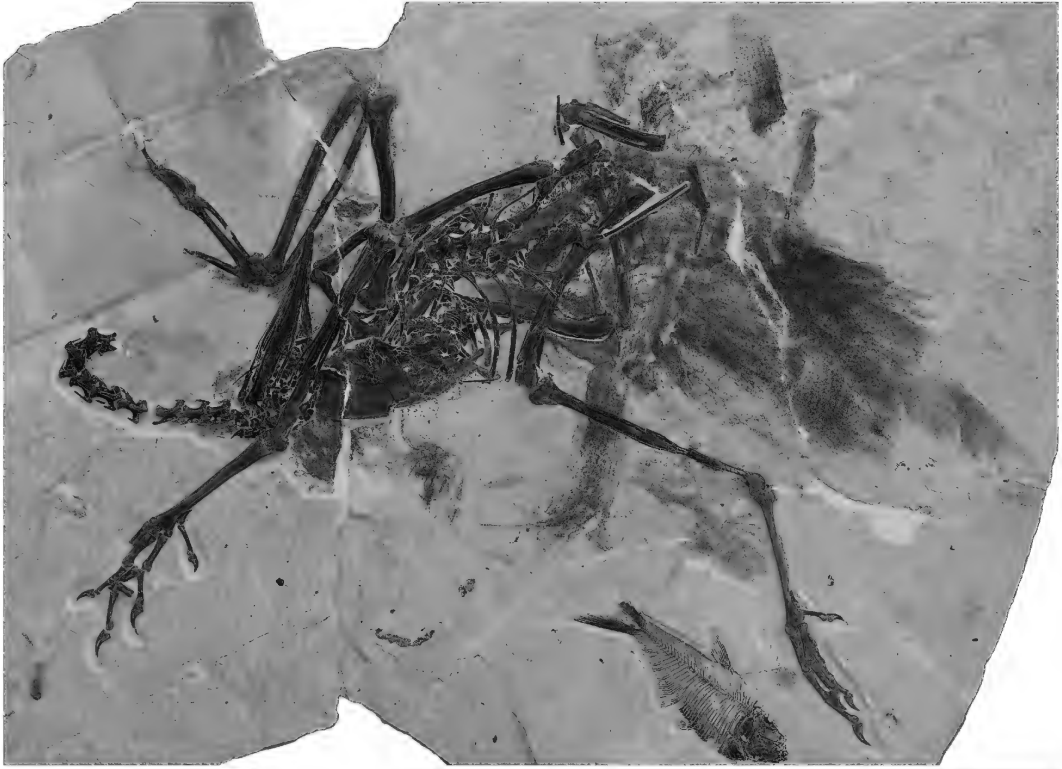
Calciavis grandei, gen. et sp. nov.

Figures 4–11

ETYMOLOGY: From *calx*, Latin for “stone” (combining form, *calci-*) *avis*, Latin for “bird,” and *grande* in honor of Lance Grande for his lifelong dedication to collecting the fauna and flora of the Fossil Butte Member of the Green River Formation. **HOLOTYPE:** AMNH 30578, essentially complete skeleton with soft-tissue preservation including feathers, pedal scales, and claw sheaths (fig. 4).

REFERRED MATERIAL: AMNH 30560, disarticulated skull, with much of the postcranial skeleton other than the femora and pelvic region. This specimen was found at the same locality as the holotype.

LOCALITY AND HORIZON: Warfield Springs (on Hebdon Ranch), locality K occurring in F-2 facies of Fossil Lake deposits (of Grande and Buchheim, 1994) of the Fossil Butte Member of the Green River Formation, near Kemmerer, Wyoming. The Fossil Butte Member is late Early Eocene, 51.66 ± 0.09 Ma (Smith et al., 2008).



DIAGNOSIS: *Calciavis grandei* is diagnosed by the following unique combination of character states: pair of distinct furrows on the anterior portion of the dentary and premaxillae (C49:1 and C2:1, respectively); lateral exposure of the ventral process of the lacrimal broad (C13:1); short fingerlike retroarticular process just posterior to the articular facets of the mandible (C60:1); sternum with slightly concave posterior margin (local autapomorphy); deep fossa posterodistal to the pisiform process on the ventral surface of the proximal portion of the carpo-metacarpus (C135:1); ischium lacking a dorsal process (C155:1); posterior portion of the ischium blunt and not tapered (C156:0); anterior margin of the preacetabular portion of the ilium flat to concave (local autapomorphy); metatarsals IV and II subequal in distal extent (C180:0).

Calciavis grandei differs from the holotype of the other Green River Formation lithornithid species, *Pseudocrypturus cercanaxius* (USNM 424078). The skull is shorter than the humerus in *Calciavis*, whereas it is longer than the humerus in *Pseudocrypturus cercanaxius* (based on the proportions of the type and comparing them to the referred specimen). *Calciavis grandei* has a proportionally narrower shaft of the coracoid and a proportionally longer tarsometatarsus than a referred specimen of *Pseudocrypturus cercanaxius* (USNM 424078). *Calciavis grandei* lacks a dorsal process on the ischium that is present in *Lithornis promiscuus* and the blunt distal end of the ischium of *Calciavis grandei* contrast with the tapering distal end of the ischium of *Lithornis plebius*. *Calciavis grandei* has a smaller preacetabular pectineal process of the pubis than that of *Lithornis celetius*. *Calciavis grandei* has less curved and more gracile scapular blade than that of *Paracathartes howardae*. *Calciavis grandei* lacks a medial flange of the pterygoid and a less developed flexor tubercle on manual phalanx III-1 in comparison with the Fur Formation lithornithid (MGUH 26770).

DESCRIPTION AND COMPARISONS

SKULL

The skull of AMNH 30578 (fig. 5) lies on its right side with the left side exposed. The left tibiotarsus lies across the orbit, hiding details of the posterior portion of the skull and much of the posterior portion of the skull roof. The skull is mediolaterally compressed in such a way that the mandibular rami abut, hindering a ventral view of the palate. The overall length of the cranium (= 84 mm) is shorter than the humerus, and differs from the other known Green River Formation lithornithid (*Pseudocrypturus cercanaxius*, USNM 424078) in which the skull is longer than humerus. The rostrum of AMNH 30578, measured from the anteriormost portion of the lacrimal (= 46 mm), is slightly greater than half the skull length (= 42 mm).

The anterior portion of the mandible overlies much of the anterior portion of the beak. Within the naris, a thin sheet of mesethmoid is present (extending well anterior to the nasofrontal hinge) to form an internarial septum, as in other lithornithids (e.g., *L. promiscuus*, USNM 391983), tinamous, and *Apteryx owenii* (AMNH 18279). The premaxillary process of the nasal is dorsoventrally thin as in tinamous (e.g., *Crypturellus undulatus*), other lithornithids (e.g., *Lithornis celetius*, USNM 290601), and ratites. The ventral (= maxillary) process of the nasal is projected at an angle about 45° to horizontal. This mediolaterally compressed process widens slightly ventrally to meet the maxilla. The ventral process of the nasal is anteroposteriorly constricted, as in other lithornithids (*Lithornis promiscuus*, USNM 391983) and tinamous. Details of the articulations among the premaxillae, maxillae, and the palate cannot be discerned. The jugal bar is somewhat rectangular in cross section with its long axis oriented dorsoventrally, slightly thickened posteriorly, and is bowed slightly ventrally ventral to the orbital region. The posterior portion is broken and dis-



FIG. 4. The holotype skeleton of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578). The bones are in white and the preserved feathers are in dark gray. Scale = 1 cm. See anatomical abbreviations.

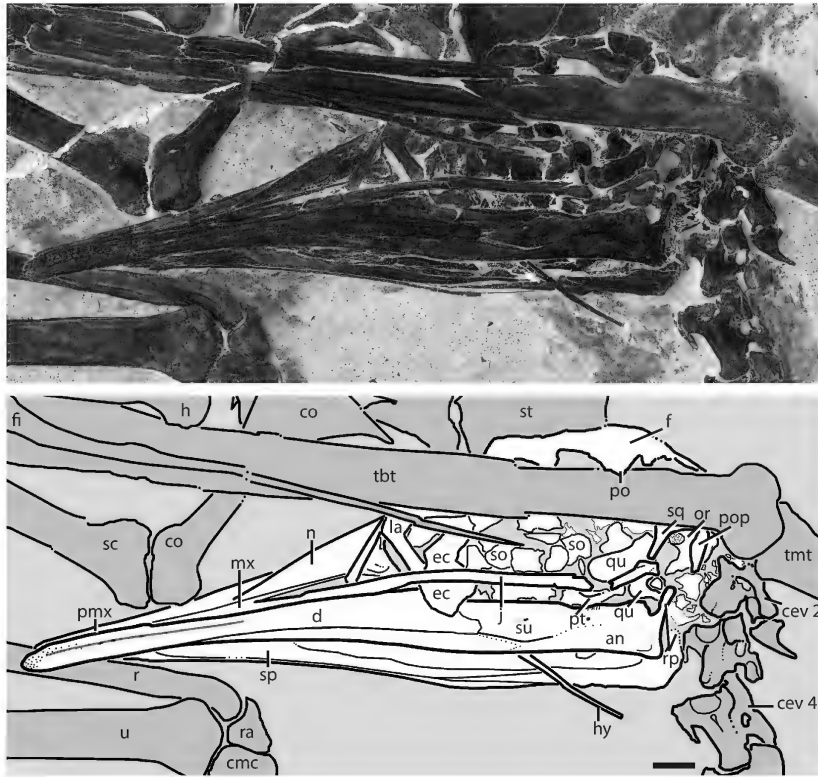


FIG. 5. The complete skull of *Calciavis grande*, gen. et sp. nov. (AMNH 30578) in left lateral view (in white). Other elements of AMNH 30578 are in dark gray. Scale = 1 cm. See anatomical abbreviations.

articulated, revealing a pitlike articular surface for the quadratojugal on the quadrate.

The lacrimal, exposed in lateral view, forms the anterior portion of the orbit. Its mediolaterally broad ventral process contacts the jugal. This flat process of the lacrimal is most similar to that of other lithornithids (e.g., *Lithornis promiscuus*, USNM 391983; *Lithornis celestius*, USNM 290601; *Pseudocrypturus cercanaxius*, USNM 336103) and contrasts with the anteroposteriorly restricted element in other palaeognaths (char. 13). It appears that the lacrimal contacted the ectethmoid, as in tinamous and in some lithornithids (e.g., *Lithornis promiscuus*, USNM 391983; *Lithornis celestius*, USNM 290601).

The large orbit contains a nearly intact sclerotic ring. The sclerotic ossicles are indistinguishable from each other in most cases, making a count of the number of ossicles impossible. No

supraorbital bones are present in AMNH 30578, and they have not been described in other lithornithids (Houde, 1988); such elements are present in tinamous (Zusi, 1993). The postorbital process is somewhat broad, like that of *Paracathartes howardae* (USNM 361415). However, the apparent breadth of the postorbital process may be exaggerated by the crushing of the endocranial cavity by the tibiotarsus. A short and pointed zygomatic process covers the lateral side of the head of the quadrate. The cranium does not appear to have dendrite-shaped furrows on the frontoparietal area as in the Messel lithornithid (IRSNB Av82; Mayr, 2009) and *Lithornis celestius*. A robust paroccipital process with a nearly flat lateral surface forms the posterior portion of the tympanic cavity. The ventral extent of the paroccipital process terminates dorsal to the mandibular articulation of the quadrate. The posterodorsal

portion of the tympanic cavity bears a well-defined fossa enclosing many tiny foramina within it, near the articulation with the head of the quadrate (= posterior tympanic recess).

The right quadrate is exposed in lateral view, but much of the lateral surface is covered by other elements. The orbital process is convex laterally, and tapers to an anteriorly rounded end. The bulbous anterior process is similar to that of other lithornithids (e.g., *Lithornis promiscuus*; USNM 336535), *Dromaeus* (TMM unnumbered), and tinamous. The posterodorsal portion of the quadrate head is partially exposed posteriorly where it meets the braincase. A disarticulated pterygoid is present anteroventral to the quadrate. The small pterygoid has an expanded, cuplike end for articulation with the quadrate. The lateral edge of the pterygoid thins into a ventrally directed flange. This thin flange indicates that a ventral pocket was present as in *Pseudocrypturus cercanaxius* (USNM 336103), *Apteryx owenii*, (USNM 18279), *Lithornis promiscuus* (USNM 391983), and *Paracathartes howardae* (USNM 391984) (Houde, 1988). The basipterygoid processes are not well exposed in this specimen, but from the morphology of the pterygoid, we deduced that the basipterygoid processes would have been posteriorly displaced unlike the more anteriorly shifted processes in galloanserines.

The left mandible is visible in lateral view (fig. 5), and the right mandible is partially visible in medial view. The height of the mandible increases posteriorly and is at its greatest height at its posterior termination. The mandibular rami are fused anteriorly in a short symphysis (~5% of mandible length). The anterior end of the mandible is laterally expanded along the dorsal margin to form a flat occlusal surface, as in all lithornithids and all other palaeognaths (Clarke, 2004). Small foramina (= foveae corporisculorum nervosorum) are present on the anterior end of the mandible, and a short anteroposteriorly oriented row lies in a shallow groove on the lateral side on the first third of the mandible. The lateral grooves extend posteriorly to the articulation with the lacrimal as a very shallow depression

and are present in lithornithids and other palaeognaths (Houde, 1988). The anterior end of the mandible does not appear to be deflected ventrally as in *Lithornis* from Messel (IRSNB Av82; Mayr, 2009) and *Lithornis promiscuus* (USNM 336535). The dentary portion of the left mandible is disarticulated and rotated dorsally. However, the well-preserved surfaces of this element allow articulations to be discerned. The posterior portion of the dentary is forked and split into distinct dorsal and ventral processes. The ventral process is more posteriorly expanded and sits in a lateral groove on the angular, as in most stem Aves, lithornithids, and palaeognaths (Clarke, 2004). The angular continues anteriorly, medial to the dentary, for nearly half the length of the mandibular ramus. The anterior extent of the angular is not discernible, and it may be partially fused with the splenial. A small projection on the dorsal portion of the surangular is interpreted to be a small coronoid process. The surangular and angular are separated by a well-defined, recurved, open suture between the two elements anteriorly that becomes closed without a visible suture posteriorly. Two small foramina are present on the lateral side of the surangular (fig. 5). Medially, the splenial is unfused to the other mandibular elements as evidenced by a ventral margin that is well separated from the dentary and a posterior portion that medially overlaps the angular. Anteriorly, the splenial reaches the mandibular symphysis, although it is not clear whether the splenial is incorporated into the mandibular symphysis as in *Apteryx owenii* (USNM 18279).

The articular region of the mandible is visible only in lateral view. The lateral mandibular condyle of the quadrate sits in a well-defined notch of the lateral side of the mandible. The anterior wall of the notch terminates dorsally in a point, and the posterior wall expands into a distinct posterodorsally projected retroarticular process that expands well above the dorsal extent of the mandible. This process is continuous with the lateral side of the mandible and is distinctly separated from the medial process, and this process is present in all lithornithids (*Lithornis promiscuus*

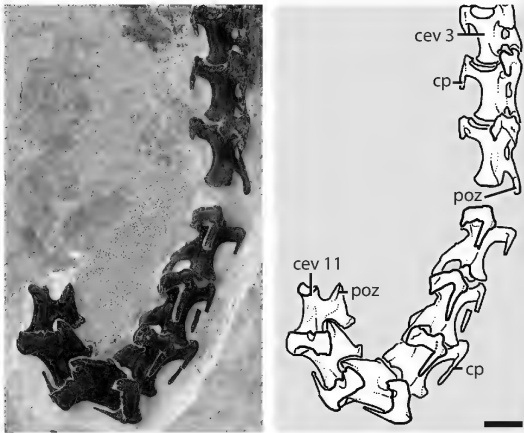


FIG. 6. The cervical vertebrae of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578) in lateral and ventral views. Scale = 1 cm. See anatomical abbreviations.

cuus, USNM 391983; *Pseudocrypturus cercanaxius*, USNM 336103; MGUH 26770; Bourdon and Lindow, 2015) with the posterior portion of the mandible exposed. As noted by Mayr (2009), this process is hypothesized to be the attachment site for the aponeurosis mandibulae medialis. The mandibular ramus terminates directly posterior to this process.

VERTEBRAL COLUMN

The presacral vertebrae are split into three sections: an articulated series consisting of presacrals 1–12 that are in articulation with the skull (figs. 5, 6); a partially disarticulated series consisting of four presacral vertebrae partially obscured by the posterior portion of the sternum (fig. 5); and an articulated series consisting of the last six presacral vertebrae (fig. 7). A total count of 22 presacral vertebrae is preserved in AMNH 30578, but it is not clear how many presacrals were present in life; 23 were estimated for the Siber and Siber lithornithid specimen (USNM 424078; Houde, 1988). All presacral vertebrae have heterocoelous articulations.

The atlas lies under the left tibiotarsus (fig. 5). The axis is preserved in lateral view and is shorter than the third cervical. Small foramina, observable in lateral view, lie on the lateral side of the

centrum just posterior to transverse foramina as in *Chauna torquata* (AMNH 1773). There are no winglike processes on the lateral side of the centra (Mayr and Clarke, 2003: char. 50), as there are in *Crypturellus undulatus*. The robust ventral process is well separated from the articular surface contacting the atlas. A deep pneumatic fossa is present on the ventral side of a lamina stretching anteriorly from the lateral side of the postzygapophysis. The neural spine is broad and low. Posteriorly, the neural arch bears slightly arched postzygapophyses. A large and rounded epiphysis (= torus dorsalis) extends posteriorly past the articular surface of the postzygapophysis.

The third cervical appears to have an osseous bridge from the transverse process to the postzygapophysis (Mayr and Clarke, 2003). The third cervical has a robust ventral process that spans the length of the ventral centrum body, whereas the fourth cervical has a low ventral process restricted to the anterior portion of the body. Ventral processes are absent in all the other preserved cervical vertebrae. The cervical vertebrae share a similar length, a depression on the posterior portion of the ventral surface, small tubercles on the ventral side of costal processes, and they lack fossae or foramina in the lateral sides of the centra. The costal processes are shorter than the length of the centrum and lack an osseous bridge connecting them with the midsection of the centrum of the vertebra (Mayr and Clarke, 2003: char. 53). The length of the costal processes in *Calciavis* is proportionally shorter than that of MGUH 26770 (referred to *Lithornis vulturinus*).

Six thoracic vertebrae exposed in ventral view (fig. 7) are loosely articulated with the synsacrum. The thoracic vertebrae do not form a notarium. A thin, anteroventrally expanded ventral process is present in the first of the articulated series (not necessarily the first thoracic vertebra). The remaining thoracic vertebrae have more abbreviated ventral processes. The transverse processes are well exposed in ventral view in the last three thoracic vertebrae. These expanded transverse processes terminate in

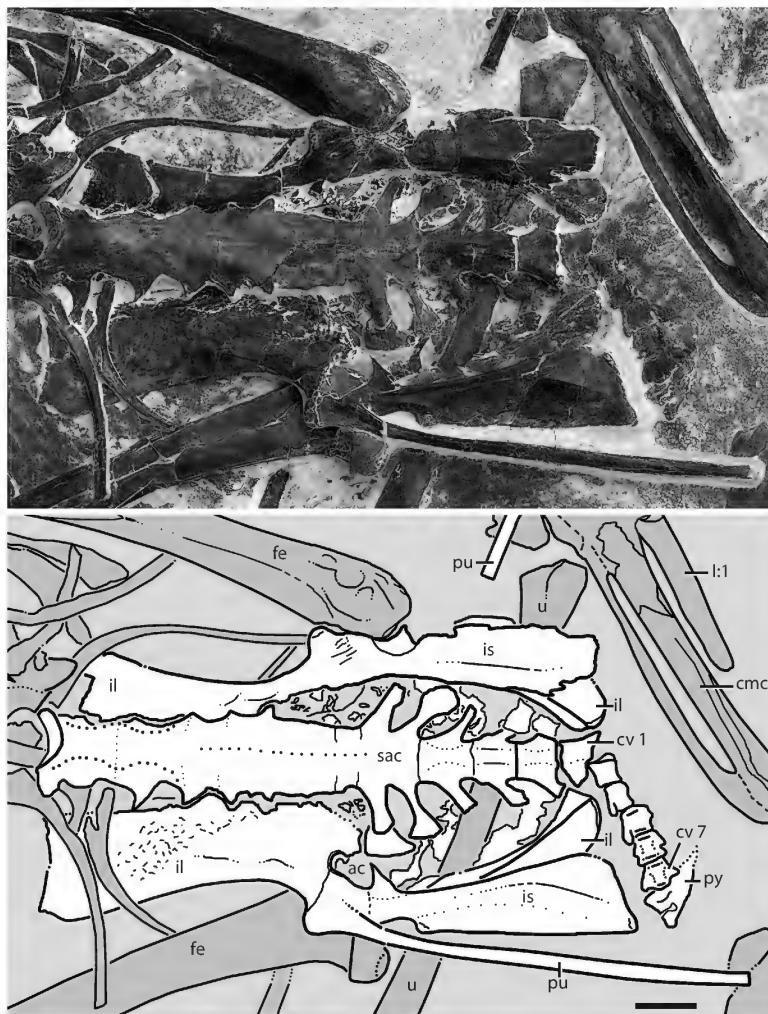


FIG. 7. The pelvic girdle, sacrum, and caudal series of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578) in ventral view (in white). Other elements of AMNH 30578 are in dark gray. Scale = 1 cm. See anatomical abbreviations.

straight lateral margins. Three deep fossae are located at the anterior, posterior, and ventral margins at the base of the transverse process. The parapophysis, located on the anterior edge of the body, is distinctly concave. Deep, anteroposteriorly elongated foramina (= central ovoid foramina of Clarke, 2004) are located in the middle of the body of the thoracic vertebrae (fig. 7), as in other lithornithids including *Lithornis plebius* (USNM 336534), *Lithornis promiscuus* (USNM 336535), *Lithornis celetius* (USNM 290601), MGUH 26770, and *Paracathartes howardae* (var-

ious USNM specimens). The foramina in lithornithids differ from the broad lateral fossae present in *Ichthyornis dispar* (YPM 1450C; Clarke, 2004) and *Paraortygoides* (Dyke and Gulas, 2002) in being much smaller and apparently perforating the body of the centra. The last thoracic vertebra of *Calciavis* is slightly shorter than that of the other thoracic vertebrae.

The synsacrum, exposed in ventral view (fig. 7), consists of 12 coossified vertebrae that can be divided into three distinct sections following Clarke (2004): anterior sacral vertebrae, a short

series of wide vertebrae with dorsally directed transverse processes (= middle sacral vertebrae), and more posterior sacral vertebrae with a morphology similar to the anterior caudal vertebrae (fig. 7). The first section of the synsacrum consists of five vertebrae with laterally directed sacral transverse processes. The first sacral vertebra bears a free rib and has a wide anterior articulation surface for articulation with the last thoracic vertebra. The width of the bodies of the sacral vertebrae increases slightly across the first five vertebrae. A slight longitudinal depression is present on the ventral midline starting on the fourth sacral and continuing through the short series of midsacral vertebrae. The middle sacral vertebrae series consists of three elements with dorsally directed transverse processes. Weak furrows and paired sacral nerve foramina define the edges of the fused centra. Three morphologically distinct midsacral vertebrae are also present in other lithornithids (e.g., *Lithornis plebius*, USNM 336534; *Lithornis promiscuus*, USNM 336535; *Lithornis celetius*; USNM 290601) and in *Ichthyornis dispar* (YPM 1450, 1732), whereas there are four in ratites, tinamous, *Apatornis celer* (Clarke, 2004), and early diverging neognaths. The first sacral in the posterior series has posterolaterally directed transverse processes that are the longest of the series. These rodlike processes contact the ilium just posterior to the acetabulum as in other avialans (e.g., *Lithornis promiscuus*, USNM 336535, tinamous, and *Ichthyornis dispar*). The posterior sacral vertebrae progressively decrease in width and increase in length.

Calciavis (AMNH 30578) preserves the first complete series of caudal vertebrae in a lithornithid (fig. 7). In total, the series is short, measuring about two-thirds the length of the synsacrum. Seven free caudal vertebrae and an incompletely preserved pygostyle comprise the caudal series. No free chevrons are present. The first two caudal vertebrae are most similar to the last vertebrae in the synsacrum and are slightly larger both in width and length as compared with that of the other caudal vertebrae. The transverse processes of the first two caudal

vertebrae are posterolaterally projected from the body like that of the last few sacral vertebrae. The next five caudal vertebrae are uniform in length and width. The anterior and posterior centrum ridges are poorly differentiated resulting in cylindrically shaped centra. Ventrally, there are no pneumatic foramina on the centrum as in some ratites (e.g., *Dromaeus novae-hollandiae*). The pygostyle is narrow and approximately equal to the length of three of the diminutive posterior caudal vertebrae; it is proportionally longer than that of *Crypturellus undulatus* (AMNH 6480). The anterior portion of the pygostyle has a single short transverse process. Its ventral process is slightly clublike, as described for *Lithornis promiscuus* (USNM 336535). An anteriorly open foramen is present at the anteroventral margin of the pygostyle as in *Lithornis promiscuus* (USNM 336535), *Lithornis plebius* (USNM 336534), and *Paracathartes howardae* (USNM 361435). The posterior end, although broken, appears to terminate in a point as in *Lithornis promiscuus* (USNM 336535). In overall form, the tail is short, lightly built, and morphologically similar to those of tinamous (Houde, 1988) and other palaeognaths (Clarke, 2002).

RIBS

The ribs from the anterior portion of the thoracic series are disarticulated, and the ribs from the posterior portion of the thoracic series are loosely articulated with their respective vertebrae (fig. 7). The ribs from the posterior portion of the thoracic series broaden ventrally, are thickened at their distal ends, and bear uncinat processes (fig. 4). The elongated uncinat processes arc posterodorsally and taper to a point. The processes are not fused to their ribs, and ribs without articulated uncinat processes have a distinct scar for articulation with the element. Although Houde (1988) makes no mention of uncinat processes, the photograph of the Siber and Siber specimen (Houde, 1988: fig. 35) appears to preserve several incomplete uncinat processes. The

remains of these processes appear consistent with smaller processes than those preserved in the holotype of the new species.

PECTORAL GIRDLE

STERNUM: The sternum, although partially crushed, is well preserved and exposed in left lateral view (fig. 4). The anterior portion of the sternum is covered. The overall proportions are similar to that of other lithornithids (e.g., *Lithornis promiscuus*, USNM 336535). The deep keel of the sternum is deepest anteriorly and terminates at the posterior extent of the element. The ventral margin of the keel is straight in lateral view. Anteriorly, the apex is short and rounded. The lateral surface of the body of the sternum is smooth, and there is no raised, paired intermuscular ridges visible parallel to the sternal midline. The posterior margin is slightly concave with no distinct posterior notches or trabeculae. The coracoidal sulci appear to cross slightly at the midline as in *Lithornis promiscuus* (USNM 336535) and there appear to be a minimum of four processes for articulation with the sternal ribs.

CORACOID: The left coracoid is preserved in ventral view (fig. 4). The midshaft is narrow like that of other lithornithids (e.g., *Lithornis promiscuus*; USNM 336535) and rapidly expands into a broad sternal margin that is dorsoventrally flattened. A lateral intermuscular ridge is present stretching from near midshaft to the lateral 1/3 of the articular facet with the sternum. The lateral process tapers to a posterodorsally directed apex as in *Lithornis promiscuus* (USNM 336535), *Lithornis plebius* (USNM 336534), and *Paracathartes howardae* (USNM 361417). Proximally, a prominent scar for the m. acrocoracoidohumeralis ligament is visible in lateral view. A distinct rounded rim surrounds this scar, and a small pit is located at the posterolateral portion. The surface of the glenoid is flat. The shape of the procoracoid process and the presence or absence of a foramen for the supracoracoid nerve cannot be determined.

SCAPULA: The left scapula remains in articulation with the left coracoid (figs. 7, 8) whereas

much of the right element is buried underneath ribs and vertebrae in the thoracic region. The scapula is at least three-quarters the length of the humerus. The proximal portion bears an elongated and oval glenoid facet. Most of the acromion is covered by other elements. The scapular shaft gradually decreases in dorsoventral width posteriorly, as in other lithornithids (e.g., *Lithornis promiscuus*, USNM 336535) and other Aves. The curvature of the shaft is more similar to that of *Lithornis promiscuus* (USNM 336535) and *Lithornis plebius* (USNM 336534) in that it is straighter than the more recurved scapula of *Paracathartes howardae* (USNM 361419). The distal tips of the scapulae are covered by other elements of the skeleton.

FORELIMB

HUMERUS: The left humerus is exposed in posterior view (fig. 8) whereas the right humerus is mostly covered by other skeletal elements (fig. 4). The humerus is slightly longer than the ulna and the shaft of the humerus is sigmoid as described by Houde (1988) for other lithornithids. Proximally, the head of the humerus is rounded and well defined. The ventral tubercle is knoblike and located at the distal margin of the humeral head, as in other lithornithids (e.g., *Paracathartes howardae*, USNM 361420; *Lithornis plebius*, USNM 336534). The dorsal rim of the pneumotricipital fossa is present distal to the ventral tubercle. A wide, mediolaterally oriented capital groove separates the humeral head from the ventral tubercle. The capital groove is open in AMNH 30578 unlike the condition in tinamous (e.g., *Crypturellus*) and galliforms (e.g., *Gallus*), where the capital groove terminates distally in a tubercle (Clarke and Chiappe, 2001). The deltopectoral crest is obscured in both humeri.

The distal ends of the humeri are slightly crushed and broken. The m. humerotricipitalis sulcus is well defined and deep. The m. scapulo-triceps groove is shallow to essentially absent in *Calciavis*, other lithornithids (Houde, 1988), tinamous, and most nonavian avialans (Clarke,

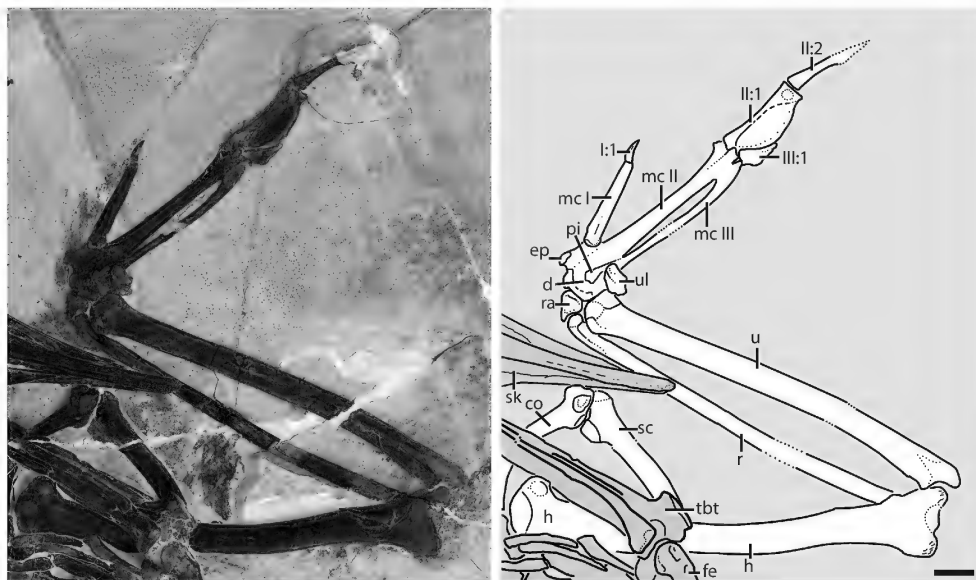


FIG. 8. Left forelimb of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578) in ventral view (in white). Other elements of AMNH 30578 are in dark gray. Scale = 1 cm. See anatomical abbreviations. See anatomical abbreviations.

2004). The flexor process is weakly projected distally, but extends just slightly distal to the ventral condyle. A dorsal supracondylar tubercle is present at approximately the same proximal height as the dorsal condyle, as in other lithornithids and tinamous. In the flightless palaeognaths, this tubercle is unsurprisingly typically reduced along with the wing musculature. A small depression lies on the proximal edge of the dorsal supracondylar process.

ULNA AND RADIUS: The left ulna is exposed in ventral view, and the proximal and distal ends of the right ulna are exposed in dorsal view (fig. 8). The bowed shaft of the ulna is slightly shorter than the humerus. This observation is consistent with most lithornithids (e.g., *Lithornis plebius*, USNM 336534; *Lithornis promiscuus*, USNM 336535; Siber and Siber specimen, USNM 424078; MGUH 26770). No conspicuous or raised feather papillae are present. However, these are preserved in the referred specimen (AMNH 30560). The olecranon process is short, but projects proximally to the cotylae. A low, elongate scar marks the attachment site for the m. biceps on the ulna. A thin rim

defines the proximal and posterior portions of the brachial depression. However, the apparent depth of the depression may be the result of crushing of the specimen. The distal portion of the ulna bears a fingerlike carpal tuber that is well separated from the distal articular surfaces of the ulna. The intercondylar sulcus is shallow as in other lithornithids and tinamous, and a sharp ridge separates the ventral ulnar condyle and the carpal tuber.

The left radius is covered proximally by the humerus (fig. 8) and the pelvis covers the right radius distally. The slender radius has an essentially straight shaft. The diameter of the radius at its midpoint is about half that of the ulna. In proximal view, the articular surface is concave and round. A distinct bicipital tubercle is present, and a small, deep pit lies next to this tubercle.

PROXIMAL CARPALS: Both the ulnare and radiale remain in articulation on the left side (fig. 8), but the wrist is disarticulated on the right side (fig. 4). The metacarpal incisure of the ulnare is deep, but it is not clear how the lengths of the rami compare to each other; in tinamous and other lithornithid specimens these rami are sub-

equal in length (Clarke, 2002). A small tuber is present on the posterior side where the dorsal and ventral rami meet as in Galloanserae (e.g., *Chauna torquata*) and in lithornithids (*Lithornis plebius*, USNM 336534; *Lithornis promiscuus*, USNM 336535). The ventral ramus bears a deep tendinal groove as is present in other Aves and *Ichthyornis dispar* (SMM 2503; Clarke, 2004).

CARPOMETACARPUS: The left carpometacarpus is exposed in ventral view (fig. 8), and the right carpometacarpus is disarticulated and exposed in dorsal view (fig. 7). The total length of the carpometacarpus is slightly more than half the length of the humerus. The slender carpometacarpus has a relatively wide metacarpal II (= major metacarpal) and straight metacarpal III (= minor metacarpal) circumscribing a narrow intermetacarpal space. The intermetacarpal space does not extend proximally to reach the distal end of metacarpal I. As in other lithornithids (Houde, 1988), metacarpal III is ventrally shifted relative to metacarpal II. Proximally, the posterior side of the carpal trochlea has a proximodistally elongated deep pit (= fovea carpalis caudalis). A similarly deep pit is also present in some Galloanserae (e.g., *Gallus*) and lithornithids (e.g., *Lithornis plebius*, USNM 336534; *Lithornis promiscuus*, USNM 336535; *Paracathartes howardae*, USNM 361445) but clearly absent in tinamous (e.g., *Crypturellus undulatus*, AMNH 6480) (Clarke and Chiappe, 2001).

The knoblike pisiform process is bordered by two fossae, one proximal and one anterior. The fossa proximal to the pisiform (fossa infratrochlearis) excavates the proximal edge of the pisiform process (Clarke and Chiappe, 2001; Clarke et al., 2006: char. 148). The pisiform process is connected to the ventral surface of metacarpal III by a distinct ridge. A tubercle is present at the proximoventral portion of metacarpal III. Most basal avians have a scar or slightly raised ridge here also. A distinct tubercle is present in AMNH 30578, *Lithornis promiscuus* (USNM 336535), *Lithornis celetius* (USNM 290554), and *Lithornis plebius* (336534), but not in *Paracathartes howardae*

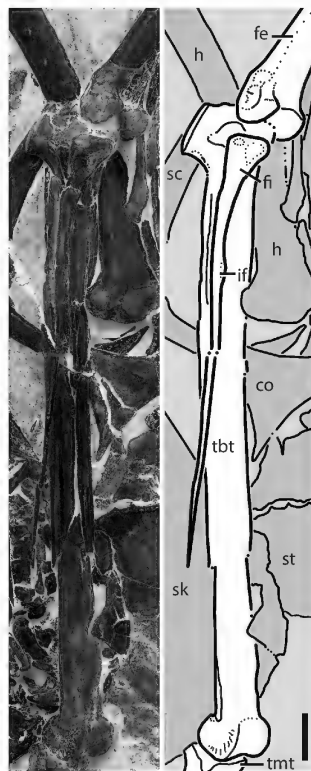


FIG. 9. The left tibiotarsus and fibula of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578) in postero-lateral view (in white). Other elements of AMNH 30578 are in dark gray. Scale = 1 cm. See anatomical abbreviations.

(USNM 361446). A deep pit just posterior to the pisiform process is present in AMNH 30578, other lithornithids (e.g., *Lithornis plebius*, *L. promiscuus*, *L. celetius*, and *Paracathartes howardae*), and tinamous (e.g., *Crypturellus*). There is no intermetacarpal process. A shallow tendinal sulcus is present on much of the dorsal surface of metacarpal II. Metacarpal III is slightly longer in distal extent than metacarpal II. A cup-shaped alular facet is present on the distal end of metacarpal I. The tip of extensor process conspicuously surpasses this facet for digit I-1 by approximately the width of the facet, producing a pronounced knob (Clarke et al., 2006: char. 144).

The length of the alular digit measures about half the length of the carpometacarpus. This digit in the Siber and Siber specimen referred to

Pseudocrypturus is considerably shorter and is roughly one-third the length of the carpometacarpus (Houde, 1988: fig. 34). The proximal articular facet is the widest portion of the alular digit in *Calciavis*, and the element tapers distally. The distal end of digit I-1 has a wide facet for the alular ungual for a total of two phalanges. The ungual is slightly posteriorly recurved, tapers to a point, and bears a lateral groove that originates near the proximal end and terminates at the tip of the element.

The second manual digit is known from the combination of preserved portions of both the left and right sides. *Calciavis* does not have a proximally directed process on the anteroventral face of the proximal end as in tinamous, *Ichthyornis dispar* (Clarke, 2004), and some Galliformes. An internal index process is not present. Phalanx II-2 is a thin element that tapers distally. The proximal portion is rounded in cross section, and a small tuber is present on its anterodorsal edge. The body of the phalanx expands slightly posteriorly at approximately its midpoint where there is a depression on the dorsal surface. A similar expansion is present in the Siber and Siber specimen (USNM 424078), but is not present in *Crax pauxi* (AMNH 4719) or *Crypturellus undulatus* (AMNH 6480). Phalanx II-2 terminates in a blunt, poorly defined articulation surface. It is not clear whether an ungual was present. However, a tiny ungual is present on digit II in the exquisitely preserved lithornithid specimen (AMNH 30560) referred to *Calciavis grandei* (see description below).

The third manual digit consists of a single phalanx III-1. This digit is short, measuring less than half the length of phalanx II-1 as in tinamous (e.g., *Crypturellus undulatus*, AMNH 6480). The short phalanx terminates distally in a rounded point. The posterior side bears a distinct flexor tubercle giving phalanx III-1 a triangular shape. This shape is in contrast to the long, rodlike phalanx III-1 of MGUH 26770 (referred to *Lithornis vulturinus*; Bourdon and Lindow, 2015).

PELVIC GIRDLE

PELVIS: The ilia, ischia, and pubes are exposed in either ventral or medial views (fig. 7). The preacetabular portion of the ilium is longer than the postacetabular portion. The anterior margin of the preacetabular portion is slightly concave in lateral view. This shape is in contrast to the distinctly convex anterior margin of most palaeognaths including *Lithornis celetius* (PU 23485) and to the straight margin of MGUH 26770, referred to *Lithornis vulturinus* (Leonard et al., 2005; Bourdon and Lindow, 2015). The anterolateral corner of the ilium is rounded and not distinctly expanded as it is in tinamous (e.g., *Crypturellus undulatus*, AMNH 6480). Scars for the attachment of the sacral ribs are present in a longitudinally oriented row near the ventral margin of the preacetabular portion, just anterior to the acetabulum. It appears that the preacetabular portions of the ilia did not contact at the midline. The ventral portion of the postacetabular portion of the ilium bears a distinct, ventral pocket for the brevis musculature. A distinct ridge for the ilioischadic membrane (Houde, 1998) is visible. It is also present in *Lithornis promiscuus* (USNM 336535) and tinamous. The posterior margin of the ilium is rounded.

The postacetabular portion of the ilium does not contact the ischium ventrally as in neognaths, and therefore, there is no enclosed ilioischadic fenestra. The posterior margin of the ischium is straight, similar to the condition in *Lithornis promiscuus*, *Apteryx*, and tinamous, but unlike specimens of *Lithornis plebius* (USNM 336534) and a specimen that was referred to *Pseudocrypturus cercanaxius* (WN 80280; Houde, 1988). The obturator foramen is open posteriorly and framed posteriorly by a distinctly rounded and robust tuber on the ventral border of the ischium. The straight ventral and dorsal edges of the ischium slightly diverge from each other posteriorly resulting in a slight increase in height posteriorly relative to the anterior portion (fig. 7).

The right pubis is completely preserved in AMNH 30578 in medial view. The pectineal pro-

cess is well developed as a knob that slightly projects anterior to its articulation with the ilium. The pectineal process is similar in shape to that of *Lithornis plebius* (USNM 336534) and *Lithornis promiscuus* (USNM 336535), but it is not as expanded anteriorly as in *Lithornis celetius* (USNM 290601) and tinamous (e.g., *Crypturellus undulatus*, AMNH 6480). The pubis is directed posteriorly paralleling the ischium, and is a third longer than the ischium. The shaft of the pubis does not contact the ischium throughout its length; it is straight, remains the same height and width posteriorly, and ends in a blunt termination. The proximal end does not appear to have a pectineal process on the ventral margin below the acetabulum as in *Lithornis promiscuus* (USNM 336535).

HIND LIMB

FEMUR: The left femur is exposed in posterior view, and the right femur is exposed in anterior view (fig. 4). The largely straight shaft of the femur bows slightly anteriorly. The trochanteric crest is only weakly projected proximally, as in other lithornithids (Houde, 1988). The rounded head of the femur has a distinct neck. Laterally, the muscle scars for the m. ischiofemoralis and the m. iliotrochantericus are deep and well developed. Prominent anterior and posterior intermuscular lines extend the length of the femur. The popliteal fossa is shallow like that of other lithornithids (e.g., *Lithornis promiscuus*, USNM 336535; and *Paracathartes howardae*, USNM 361412). The distal condyles are approximately equal in distal extent. The medial condyle is set well apart from the shelflike lateral and tibiofibularis crests. The posterior surface of the medial condyle is nearly flat.

TIBIOTARSUS: The left tibiotarsus is exposed in posterolateral view (fig. 9), and the right tibiotarsus is in medial view (fig. 4). Proximally, the anterior and lateral cnemial crests are weakly projected proximally and anteriorly, respectively. The anterior cnemial crest is slightly longer than that of the lateral crest, but the lateral crest is

more projected. The base of the anterior crest is slightly anteriorly expanded. A similar expansion is present and much more developed in *Lithornis plebius* (USNM 336534). As in *Crypturellus undulatus*, the base of the anterior cnemial crest of AMNH 30578 forms a distinct obtuse angle with the shaft. The lateral cnemial crest is thickened distally into a flat lateral surface of the tibia. The lateral articular surface is concave. The lateral side of the shaft bears a sharp, elongated fibular crest on the lateral side that extends for a length about one-fourth the length of the element. Distally, the medial condyle projects further anteriorly than the lateral condyle, but it is difficult to compare the relative size of the two condyles given their angle of preservation. The intercondylar sulcus is wide, shallow, and defined proximally. An extensor (= tendinal) groove is present and positioned proximomedial to the intercondylar space and exits nearly adjacent to the proximal edge of the medial condyle. There is no ossified supratendinal bridge as in most nonavian avialans (e.g., Clarke, 2004), lithornithids (Houde, 1988), some ratites (Cracraft, 1974), and owls. The position of the groove in *Calciavis* (AMNH 30578) and other lithornithids is similar to that of tinamous and other palaeognaths with a supratendinal bridge.

FIBULA: The left fibula is exposed in lateral view (fig. 9). The element tapers distally and is approximately three-quarters the length of the tibiotarsus. Proximally, the fibula is asymmetrical in lateral view with the posterior portion is more pointed than the anterior margin. Its anterodorsal corner bears a deep pit. A similar scar also is present in *Crypturellus undulatus* (AMNH 6480), but is located more anteriorly. Another depression is located on the lateral side of the proximal end. The m. iliofibularis attachment is located on the posterior margin and is developed as a thin flange with a rugose distal end.

TARSOMETATARSUS: The right tarsometatarsus is preserved in medial view (fig. 10), and the left tarsometatarsus is in plantar view (fig. 11). The proximal tarsals are completely fused with the metatarsals without a visible suture. A small ses-

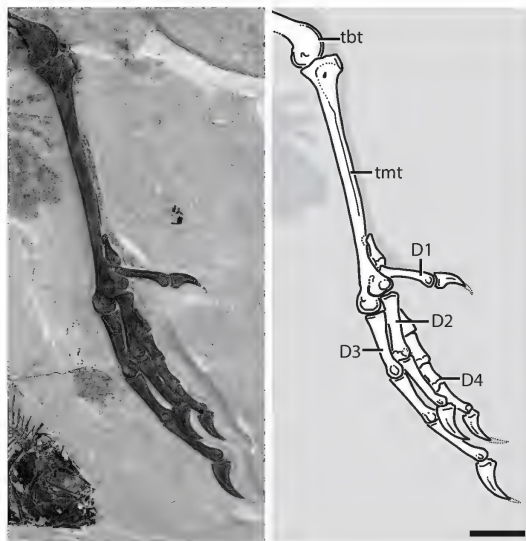


FIG. 10. The right pes of the holotype of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578) in medial view. Note the preservation of pes scales on the posterior/plantar portion of the pes, feathers, and the claw sheaths (all in dark gray). Scale = 1 cm. See anatomical abbreviations.

amoid is present proximal to the planter portion of the tarsometatarsus. The hypotarsus is proximodistally short and expanded plantarly with a weakly projected medial crest and no enclosed canals as in all known lithornithids (e.g., *Lithornis promiscuus*, USNM 336535; *Lithornis plebius*, USNM 336534; *Paracathartes howardae*, USNM 361406). Similarly sized, paired proximal vascular foramina exit at approximately the same proximodistal level on the plantar surface. Medial and lateral plantar crests frame a shallow sulcus extending much of the length of the tarsometatarsus. Metatarsal I is short and articulates with the medioplantar side of the tarsometatarsus at a very slight depression; it is proximally tapered with a blunt apex.

Trochlea II and IV are dorsoplantarly rounded. Trochlea III is ginglymoid, whereas trochlea II and IV have very weak to absent furrows. The articular surface of trochlea III is symmetrical in plantar view and poorly expanded proximally. In *Lithornis plebius* (USNM 336534), *Lithornis promiscuus*, (USNM 336535), and



FIG. 11. The left pes of the holotype of *Calciavis grandei*, gen. et sp. nov. (AMNH 30578) in plantar view. Scale = 1 cm. See anatomical abbreviations.

Paracathartes howardae (USNM 361406), trochlea III is slightly asymmetrical in plantar view. The distal extent of trochlea II and IV of *Calciavis grandei* are equal. The distal vascular foramen and distal interosseus canal are small, and exit plantarly and distally, respectively. Small subcircular structures adjacent to the posterior side of the right tarsometatarsus likely represent scales preserved as carbonized traces (fig. 10).

PEDAL DIGITS: The digits are articulated in the right pes and slightly disarticulated in the left pes (figs. 10, 11). Generally, the phalanges are elongated and gracile, and the distal ends are ginglymoid. The most proximal phalanges in each digit are the longest in the series. Phalanx digit I-1 has the smallest shaft diameter. Pedal phalanx VI-4 is longer than that of phalanx IV-2 and IV-3, and phalanx III-3 is slightly longer than phalanx III-2. The unguals have a curvature of $\sim 30^\circ$ measured from dorsal surface. There is a small flexor tubercle and deep lateral grooves are present. Remains of keratin indicate that the claws were $\sim 30\%$ longer than the bony portion of the unguals.

SOFT TISSUE

FEATHERING: The feathers are preserved as carbonized traces and impressions in the matrix (figs. 4, 7, 8, 10). Disorganized patches of feathers lie near the pectoral and pelvic girdles. The patches range in size from 20 to 40 mm in diameter. Both forelimbs have remiges associated with them. The left wing looks intact, but the impressions and traces have been damaged. The feather

attached to manual phalanx I-1 and I-2 measures 76 mm and is parallel to the shaft of the phalanges. A primary feather associated with manual phalanx II-2 lies parallel to manual digit II. Other primary feathers are present, but further details cannot be discerned.

The preservation of the right wing feathering is better than that of the left and barbules can be discerned in several primaries. The number of primary feathers in this specimen is not clear. An unspecified number of primary and secondary feathers lie on top of each other and little can be discerned about individual feather lengths. It is unclear whether tail feathers are preserved because parts of the right wing feathering cover the caudal area (fig. 4).

REFERRED SPECIMEN OF *CALCIAVIS* *GRANDEI*, AMNH 30560

Figures 12–15

LOCALITY: Warfield Springs (on Hebdon Ranch), locality K occurring in F-2 facies of Fossil Lake deposits (of Grande and Buchheim, 1994) of the Fossil Butte Member of the Green River Formation, near Kemmerer, Wyoming.

PRESERVATION: AMNH 30560 is well preserved but mostly disarticulated (fig. 12). The skull and abdominal regions have disarticulated completely. The pelvic region, tail, and left hind limb are missing. It is identical in all compared morphologies and close in proportions to the holotype of *Calciavis grandei* (table 1).

SKULL: The skeleton of AMNH 30560 preserves particular details of the skull (fig. 13), forelimb (figs. 14, 15), and pectoral girdle (fig. 14) that AMNH 30578 does not and those regions are described here to supplement the description of *Calciavis*. The skull has disarticulated at approximately its midpoint. The “anterior portion” consists of the mandible, nasals, and premaxillae and the posterior portion comprises the braincase and surrounding elements; the quadrates have been displaced and are near the posterior portion of the premaxilla (fig. 13). The premaxillae are exposed in dorsal view. Anteri-

orly, deep grooves extend posteriorly from the tip of the rostrum. These grooves are present in lithornithids (e.g., *Lithornis promiscuus*, USNM 336535) and other palaeognaths. The external surface of the premaxilla is covered with small foramina. The anterior tip of the rostrum is slightly curved ventrally, unlike that of the holotype. Both quadrates are well preserved (figs. 13, 14); the left element is in lateral view and the right element is in medial view. The quadratojugal cotyla is deep. Anteriorly, the orbital process is broad dorsoventrally. A distinct, flat surface marks the articulation with the unsegmented pterygoid-palatine. It is unclear whether there are small foramina on the posterior surface of the otic process as in other early palaeognaths (see below). A distinct depression is located on the posterior surface of the body of the quadrate between the condyles and the otic process. A similar depression is present in other lithornithids including *Lithornis celetius* (USNM 290601), *Lithornis promiscuus* (USNM 336535), and *Lithornis plebius* (USNM 336534), but not in *Paracathartes howardae* (USNM 424067).

Both of the unsegmented pterygoid-palatines are preserved, but they are disarticulated from the other palatal elements and displaced from the rest of the skull (fig. 13). The right pterygoid-palatine is in dorsal view, located underneath the cervical vertebrae (fig. 13), and the left pterygoid-palatine is in ventral view, positioned under the left scapula. The pterygoid bears an anteroposteriorly elongated flat articulation surface for articulation with the basipterygoid process. The posterior portion has a shallow cuplike articular surface with the quadrate. In ventral view, there is an expanded lamina on the lateral surface of the pterygoid-palatine that bounds a ventral fossa. The articulation for the vomer cannot be observed on either side. The anteriormost portion of the elongate left vomer is visible, and its length suggests that there was vomer-premaxilla contact in AMNH 30560. However, the anterior portion of the vomer tapers, and there does not appear to be an articular facet. Therefore, it is considered uncertain whether there was vomer-

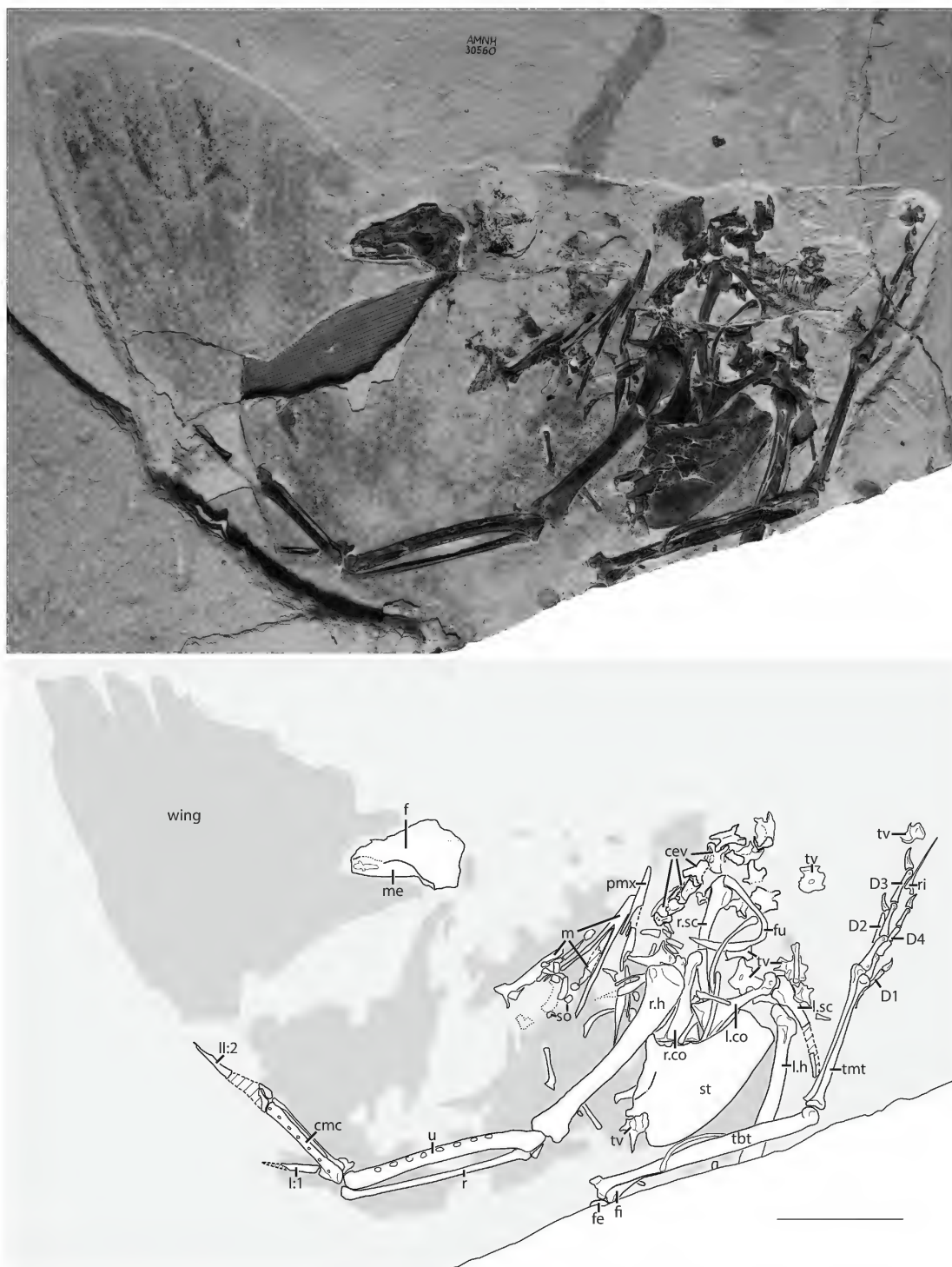


FIG. 12. The largely disarticulated skeleton of AMNH 30560 (white elements) with feather impressions (in gray). Scale = 5 cm. See anatomical abbreviations.

premaxillary contact. The basipterygoid processes are not well exposed in this specimen.

The frontal and parietal regions of the braincase are heavily crushed and distorted, and thus, few details can be discerned. The mesethmoid expands anteriorly into a dorsal process that is located just posterior of the contact between the nasals and the frontals. The position of the anterior portion of the mesethmoid is consistent with its extent anterior to the nasofrontal hinge into an internarial septum as in other lithornithids (e.g., *Lithornis promiscuus* USNM 391983), tinamous (e.g., *Eudromia elegans*, USNM 345096), and kiwis (e.g., *Apteryx owenii*, USNM 18279).

The anterior portion of the mandible is exposed in dorsal view and the posterior portion is in lateral view (fig. 13). The mandibular symphysis is identical in length to the holotype and dorsally flat as in all palaeognaths, including lithornithids (e.g., *Lithornis promiscuus*, USNM 336535). A single row of mental foramina is present on the dentary. At the posterior margin of the mandibular symphysis, a thin shelf is present just dorsal to an anteriorly extending pit as in *Lithornis promiscuus* (USNM 336535) *Paracathartes howardae* (USNM 361437), and tinamous (e.g., *Crypturellus undulatus*, AMNH 6480). It is not clear whether there are one or two foramina within this pit (Clarke, 2002, 2004). The long, disarticulated splenial appears to stretch to the mandibular symphysis, but does not appear to have contacted its contralateral twin.

POSTCRANIA: The postcrania of AMNH 30560 is well preserved and, for the most part, disarticulated (fig. 12). The cervical vertebrae are identical to AMNH 30578 in all respects. The thoracic vertebrae have a distinct pleurocoel in the lateral side of the centrum as in other lithornithids (Houde, 1988) and the holotype specimen. The medial sides of the ribs have small ridges and fossae; these characters suggest that the ribs are pneumatized.

The sternum, exposed in lateral view, bears a straight to slightly concave posterolateral margin as in the holotype. In neither specimen does the sternal midline extend significantly farther posteriorly than the lateral edges of the sternum. In

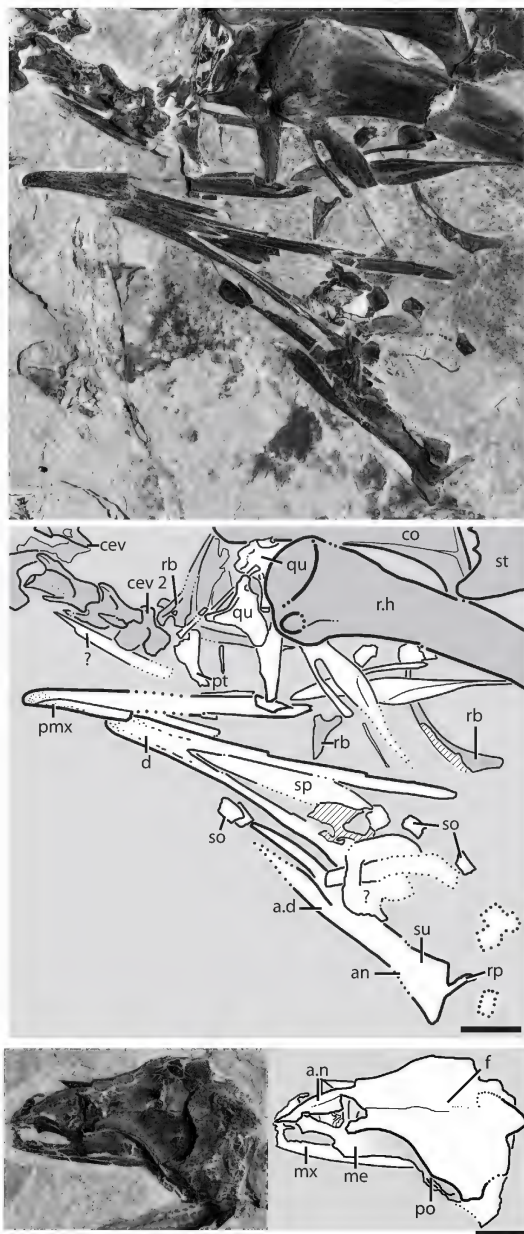


FIG. 13. The largely disarticulated skull of AMNH 30560. A, mandible and portion of the beak and B, the posterior portion of the skull. Scales = 1 cm. See anatomical abbreviations.

other lithornithids with preserved sterna (e.g., *Lithornis promiscuus*, USNM 336535, *Lithornis celetius*, PU 16961) the sternal midline extends proportionally further and the posterior margin of



FIG. 14. The pectoral girdle and humeri of AMNH 30560. The pectoral and humeri are in white whereas other elements of the skeleton are in dark gray. Scale = 1 cm. See anatomical abbreviations.

the sternum is tapered toward this midline (rather than blunt in *Calciavis*). The external spine (spina externa) is narrow, pointed, and projected anteriorly; the internal (dorsal) morphology of this part of the sternal rostrum is not visible. The coracoidal sulci appear to cross slightly at the midline as in the holotype specimen, *Lithornis promiscuus* (USNM 336535), *Ichthyornis dispar* (Clarke, 2004), and *Iaceornis marshi* (Clarke, 2004). Either four or five costal processes are present on the lateral edge of the sternum. The furcula is preserved in anterior view. The morphology of the furcula of AMNH 30560 is similar to that of the Siber and Siber specimen (USNM 424078) in that both are broadly U-shaped, a projected apophysis is absent, and the omal end seems to be unexpanded and mediolaterally compressed. The coracoids are both preserved in the same view as that of AMNH 30578. A small lateral process is present. The proportions of the coracoids of AMNH 30578 and AMNH 30560 are identical (table 1).

The scapulae are better exposed in AMNH 30560 than in the holotype (AMNH 30578). Both scapulae of AMNH 30560 are preserved in lateral view (fig. 14). The acromion extends well anterior to the glenoid and is strongly deflected laterally. The base of the acromion is smooth bone whereas the tip of the process has many small striations. As in all lithornithids, the acromion is strongly recurved and bears a distinct foramen on the posterolateral surface of its base. The blade of the scapula is straplike and tapers distally. The distal ends of the both scapulae are covered by other elements.

The forelimb of AMNH 30560 is very similar to that of AMNH 30578. The pneumotricipital fossa of the humerus is deep and located just distal to the ventral tubercle. The capital incisure is open distally. The distal end of the bicapital crest bears a shallow, posterodistally directed fossa as in tinamous and *Ichthyornis* (Clarke, 2004). The exposed base of the deltopectoral crest shows

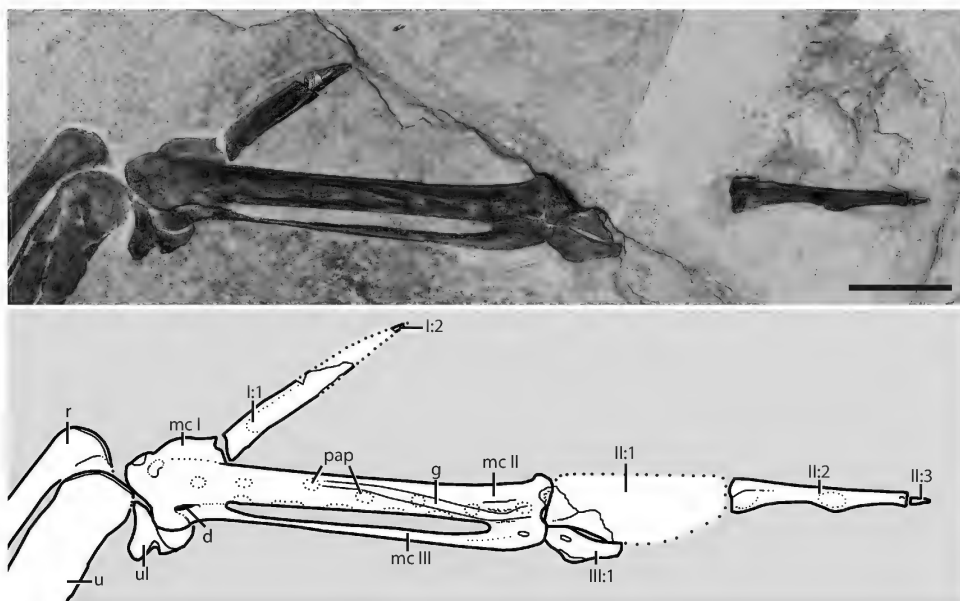


FIG. 15. The right manus of AMNH 30560 in dorsal view. Scale = 1 cm. See anatomical abbreviations.

that the deltopectoral crest extended about one-third the length of the humerus. The ulna has at least nine very slightly raised small papillae for the ligamentous attachment of secondary feathers. They are primarily demarcated by a shift in the preserved color of the bone. These marks are evenly spaced and occur as white, rough-textured scars that continue onto metacarpal II (= major metacarpal) of the carpometacarpus (fig. 15). The extensor process of the carpometacarpus is not well exposed.

Other than slight proportional differences between the tarsometatarsus and the tibiotarsus with that of AMNH 30578, the morphology of the preserved hind-limb elements are identical (table 1).

OTHER NEW GREEN RIVER FORMATION LITHORNITHID SPECIMENS

Lithornithidae
FMNH PA 729

Figure 16

LOCALITY: Thompson Ranch (locality H, F-2 deposits of Grande and Buchheim, 1994) within the Fossil Lake deposits of the Green River Formation, near Kemmerer, Wyoming.

PRESERVATION: The specimens consist of a complete, articulated left forelimb with an articulated scapula and coracoid. Parts of the forelimb (e.g., metacarpal II, coracoid) are missing, but impressions of those missing segments still remain in the matrix. The specimen is crushed, but preserves faint impressions of the wing feathering.

DESCRIPTION: The left coracoid is preserved in dorsal view and, unfortunately, much of the glenoid region of the element is not well preserved. A lateral process is not preserved. The dorsal surface of the coracoid is concave. The medial edge tapers to a thin point. The scapula is preserved in medial view, although the proximal portion and the distal extremity are missing. The coracoidal tubercle is convex, as in other lithornithids. The shaft of the scapula gradually tapers like that of *Lithornis promiscuus* (USNM 336535) and AMNH 30560, rather than that of FMNH PA 739. The length versus width and arc of curvature of the shaft of the scapula is similar to that of *Lithornis promiscuus* (USNM 336535) and AMNH 30560, rather than the more robust and curved shaft of *Paracathartes* (USNM 361419). The acromion, crushed under the coracoid, is pointed and recurved as in other lithornithids.

TABLE 1
Measurements (in mm) of individual elements of the Green River Formation lithornithids.
 See institutional abbreviations.

taxon	<i>Calciavis</i>	<i>Calciavis</i>	<i>Pseudocrypturus</i>	<i>Pseudocrypturus</i>			
Specimen #	AMNH 30587	AMNH 30560	USNM 336103	Siber	FMNH PA 739	FMNH PA 729	WGS U1b-2001
Cranium length	86.2	79.9	95.6	96.2			
Mandible length	77.3	64					
Sacrum length	62.2				57		
Sternum length	66.2	63.9		77.2			
Humerus length	91.6	81.8		84.4		90.6	
Radius length	83.5	74.9		74.5		85.8	69.4
Ulna length	87.1	79.7		79.2		86.6	75.3
Carpometacarpus length	47	41.1		42	42.5	48.5	
Phalanx length I-1	20.4	17.5		17	17.6	21.4	
Phalanx length I-2	5.4	2		6.5	4.7		4.8
Phalanx II-1	19.5				18.4	20.2	18.2
Phalanx II-2	20.3	19.4			17.9	22.4	16.5
Femur length	70.9			63	64.2		59.4
Tibiotarsus length	105.9	92.3		90.3	86.5		87.1
Tarsometatarsus length	61.2	57.9		48.1	49.3		56.3
Pedal phalanx I-1	13.1	11.5		12.4	12.8		10.9
Pedal phalanx I-2	7.1	6		8	6.6		6.4
Pedal phalanx II-1	16.1			15.2	15.4		13.2
Pedal phalanx II-2	14.5			14	14.4		10.8
Pedal phalanx II-3	9.7	7.3		10	7.6		7.3
Pedal phalanx III-1	16.5	15.1		14.1	14.8		14.3
Pedal phalanx III-2	14.7	13.4		13.8	13.3		11.9
Pedal phalanx III-3	15.9	14		14.9	14.9		12.8
Pedal phalanx III-4	10.6	9		10.9	9.5		8.5
Pedal phalanx IV-1	10.8	10		10	10.1		9.7
Pedal phalanx IV-2	8.2	7.5		7.7	7.6		6.1
Pedal phalanx IV-3	6.9	6.6		7	6.8		4.7
Pedal phalanx IV-4	10.1	8.1		9.2	9.2		6.6
Pedal phalanx IV-5	7.8	6.2		8.9	6.9		6.1

The humerus lies in posterodorsal view and has a sigmoid-shaped shaft. The proximal surface is well rounded, and there is broad capital incisure between the head of the humerus and the ventral tubercle. The deltopectoral crest is weakly

expanded anterodorsally and distally grades smoothly into the shaft. Much of the distal portion of the humerus is covered by the ulna or matrix. Proximally, the ulna bears a low olecranon process. Distally, its dorsal condyle has a flat

distal margin and a weakly developed tendinal pit. A paired series of slightly raised scars on the posterodorsal side of the ulna represent the anconal and inner papillae for the attachment of feathers. There appears to be 10 pairs of papillae that stretch from the proximal to the distal end (fig. 16). The proximal portion of the radius is mostly covered, but a pronounced bicapital tubercle is present near the proximal surface. The shaft of the radius is straight, and the shaft of the ulna has a low arc. A distinct muscular ridge is present on the posterodorsal edge of the radius for the length of the element.

The manus lies in dorsal view. The proximal carpals are largely buried in matrix. The carpometacarpus has a distinct pit (= supratrochlear fossa) on the dorsal surface just distal to the carpal trochlea. Both metacarpals II and III have straight shafts enclosing a narrow intermetacarpal space, although much of metacarpal II is preserved only as an impression (fig. 16). Metacarpal III just surpasses metacarpal II in distal extent, and the shaft of metacarpal III is “twisted” (Houde, 1988). Phalanx I-1 is the same relative length as that in the holotype of *Calciavis* and articulates with a small ungual. Phalanx II-1 is poorly preserved and lacks an index process on the distal end. Like tinamous and lithornithids, phalanx III-1 is less than half the length of phalanx II-1, and is triangular, as a result of possessing a large flexor process. The shaft of phalanx II-3 tapers and has a posterior expansion at approximately its midpoint, but the expansion is not as great as that present in the *Calciavis* holotype and the referred specimen AMNH 30560.

FEATHERING: The feathers are preserved as faint impressions in the matrix without carbonized traces, as in all the other Green River Formation lithornithids. A detailed account of feathering in this specimen was presented in Torres and Clarke (2011).

PHYLOGENETIC ASSIGNMENT: FMNH PA 729 was found within Lithornithidae in our phylogenetic analysis (see below). The poor preservation of the preserved elements inhibits the assignment of FMNH PA 729 to a species-level taxon.

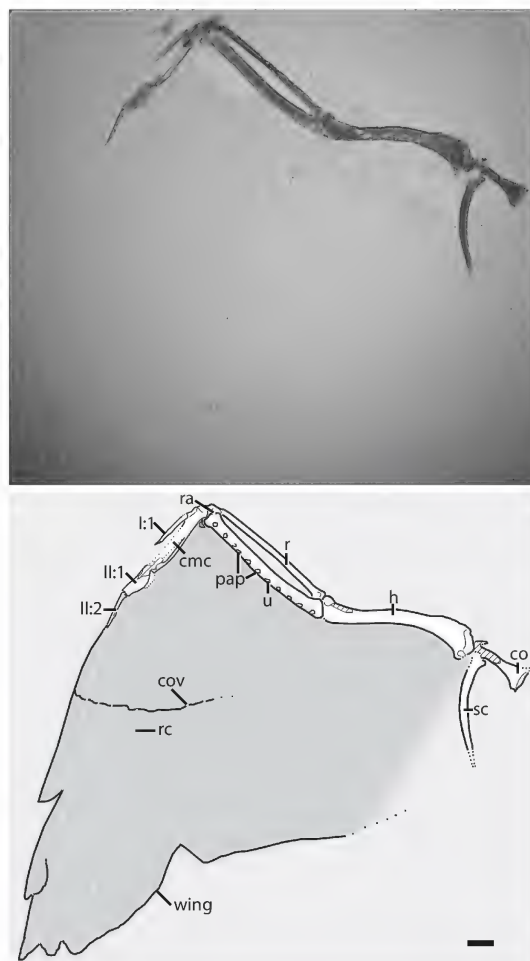


FIG. 16. The left forelimb of FMNH PA 729 in dorsal view with exquisite preservation of the covert and primary feathers (in dark gray). Scale = 1 cm. See anatomical abbreviations.

The limb proportions, absolute size, and observable morphology are consistent with other lithornithids especially AMNH 30578 (see table 1), but there are no unambiguous character states or a unique combination of character states linking the specimen to *Calciavis grandei*. Furthermore, phalanx III-1 of the manus is short and triangular like that of lithornithids, but this character state is also in other palaeognaths (e.g., tinamous). Therefore, we assign this specimen to Lithornithidae and this is supported in the phylogenetic analysis (see below).

FMNH PA 739

Figures 17–19

LOCALITY: Thompson Ranch (locality H, F-2 deposits of Grande and Buchheim, 1994), within the Fossil Lake deposits of the Green River Formation, near Kemmerer, Wyoming.

PRESERVATION: The specimen consists of much of an articulated skeleton, missing the posterior two-thirds of the skull, much of the pectoral girdle, the crux region of the left wing, and much of the right wing. No feathers are preserved, but small traces of the ungual sheaths are preserved. Some regions are well preserved, but many of the long bones are badly crushed. Some portions of the skeleton partially deteriorated before fossilization (e.g., the pygostyle), and as a result some of the details cannot be discerned.

DESCRIPTION: Only parts of the back of the skull and the anterior third of the skull were recovered with FMNH PA 739 (fig. 18). The anterior portion of the skull is crushed dorsally where only the dorsal portions of the nasals, premaxillae, and the occlusal margin of the mandible are visible. The anteriorly tapering and robust nasal bar is similar to that of other palaeognaths. The lateral sides of the premaxillae bear furrows anterior to the external naris as in other palaeognaths (Mayr and Clarke, 2003). Small foramina in a single anteroposteriorly oriented row dot the flat occlusal margin of mandible (fig. 18), a character state present in lithornithids (e.g., *Paracathartes*), *Apteryx* (USNM 18279), and some neognaths (e.g., *Gallus*).

The cervical vertebrae are missing in the specimen, and the thoracic vertebrae are scattered near the pelvis and forelimb (fig. 17). The vertebrae have clear heterocoelous articulations and neural spines equal to the height of the centrum. A distinct foramen is present in the lateral side of the centrum as in other lithornithids (see above). A notarium is not present. Thoracic ribs are mediolaterally broad and bear small crenulations on the anterior and posterior surfaces, features associated with pneumaticity. The dorsoventrally flattened synsacrum is composed of a minimum of 10 vertebrae, and the anterior

centrum bodies are longer than those of the more posterior ones. The articulations with the ilium are difficult to discern. The caudal vertebral series terminates in a small pygostyle. Individual centrum bodies are poorly preserved. However, they visibly decrease markedly in size posteriorly as in extant palaeognaths. The pygostyle is too poorly preserved to compare in detail to other lithornithids.

The sternum is crushed in left lateral view, and the anterior portion and left lateral edge are missing. A deep ventral keel is present, and a minimum of four sternal ribs attach to the sternum. It is not clear whether the posterior edge of the sternum was straight or concave. Only the distal end of the scapula is preserved. The scapula terminates in a blunt, gently rounded distal end; this character state is shared with AMNH 30560, but absent in the more tapered scapulae of FMNH PA 739 and the holotypes of *Lithornis promiscuus* and *Lithornis plebius*.

Both humeri are preserved, but severely crushed. The left humerus is in anterior view, whereas the remains of the right humerus are in posterior view. The base of rounded humeral head bears a shallow acrocoracoid ligament furrow on its anteroventral margin. Distally, the humeral condyles are about equal in size and well rounded. A distinct dorsal tubercle is present, as in other lithornithids (Houde, 1988; Clarke and Chiappe, 2001). The proximal ends of the left ulna and radius are in near articulation with the humerus (fig. 17). The olecranon process of the ulna is distinct but short. The radius has an articulation surface for the ulna distally. The proximal radius bears a distinct bicipital scar.

Parts of the left manus are preserved. Metacarpals II and III (major and minor, respectively) are parallel. There does not appear to be any expansion of the distal end of the articular surface of phalanx II-1 into an index process. Phalanx III-1 is triangular and less than half the length of phalanx II-1, as in tinamous and other lithornithids. Phalanx II-2 tapers anteriorly, but bears a distinct expansion, as in AMNH 30560. A small ungual is present on the tip of phalanx I-1.

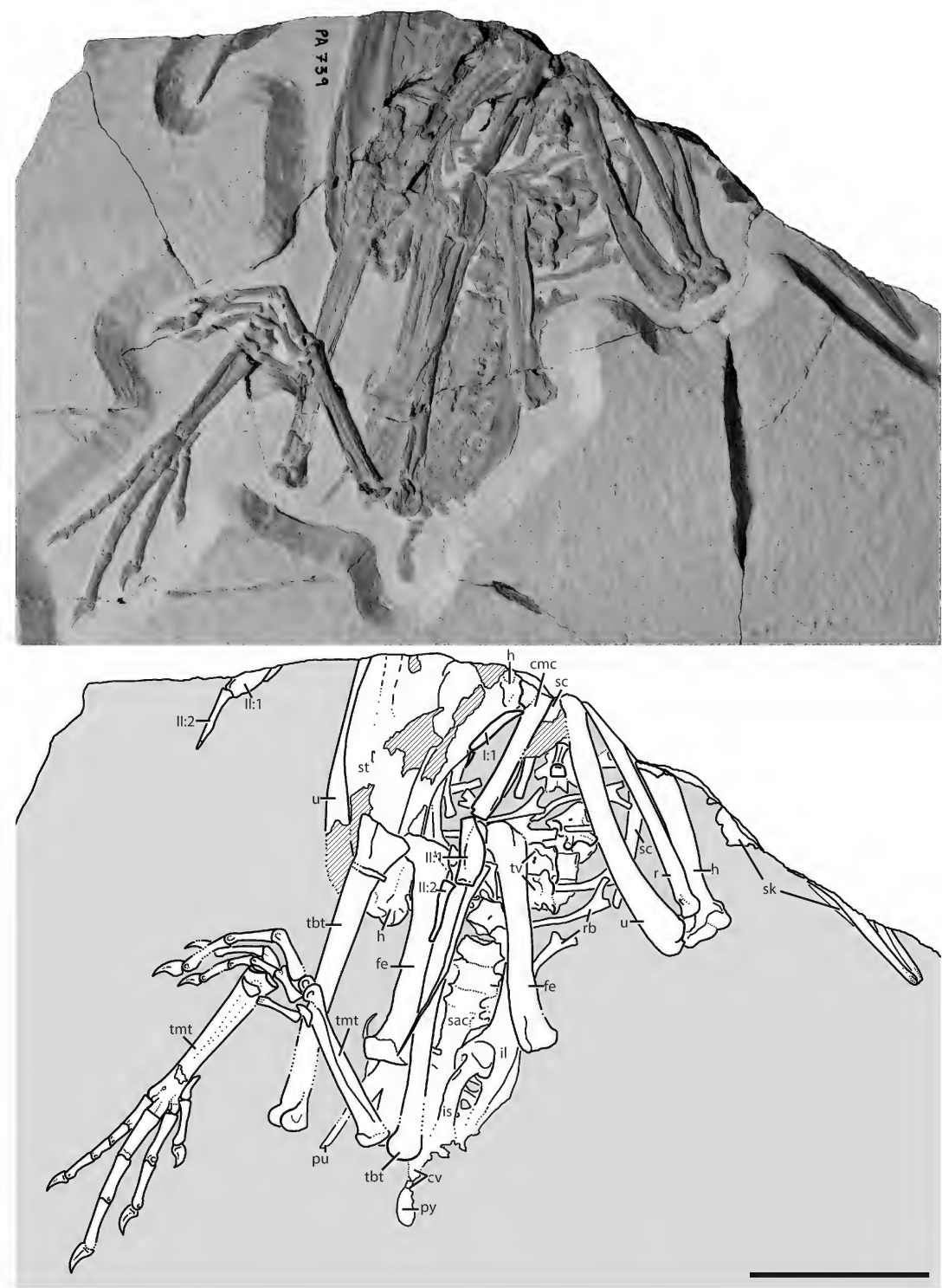


FIG. 17. The incomplete skeleton of FMNH PA 739. Scale = 5 cm. See anatomical abbreviations.

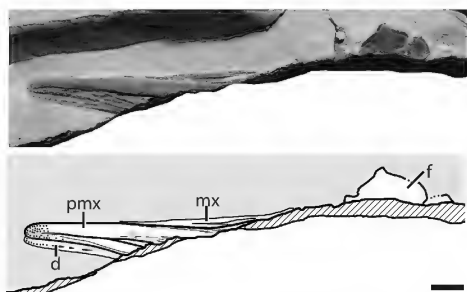


FIG. 18. The partial skull of FMNH PA 739 in dorsal view. Scale = 1 cm. See anatomical abbreviations.

The pelvic region is crushed. The preacetabular portion of the ilium is longer than the tapering posterior portion. The acetabulum is round in lateral view, and the antitrochanter is not expanded posterior of the posterior margin of the ischial peduncle, as in the holotype of *Lithornis promiscuus* (USNM 336535). The ischium and the ilium do not contact distally to enclose an ilioischiatric fenestra, as in other palaeognaths. The distal end of the pubis tapers to a point.

The femora are poorly preserved. The neck of the femur is poorly preserved, and the lateral surface of the proximal surface is not well expanded proximal to the head. The shaft of the femur is straight, and the distal ends are heavily crushed. The proximal ends of the tibiotarsi are either hidden or severely crushed. The distally tapering fibula is about three-quarters of the length of the tibiotarsus. Distally, an ossified supratendinal bridge appears to be absent. The pedes are well preserved (fig. 19) and have overall similar proportions to that of the other Green River Formation lithornithids (table 1). The plantar portion of the tarsometatarsus bears one proximodistally extensive lateral hypotarsal ridge and a relatively smaller medial hypotarsal ridge.

PHYLOGENETIC ASSIGNMENT: FMNH PA 739 was found within Lithornithidae in our phylogenetic analysis (see below). Only a portion of the skull is present, so we are unable to estimate cranial or rostral length with confidence. Hence, we cannot confidently assign FMNH PA 739 to either *Calcivis grandei* or to *Pseudocrypturus cercanaxius*. The limb proportions are similar to that of the referred

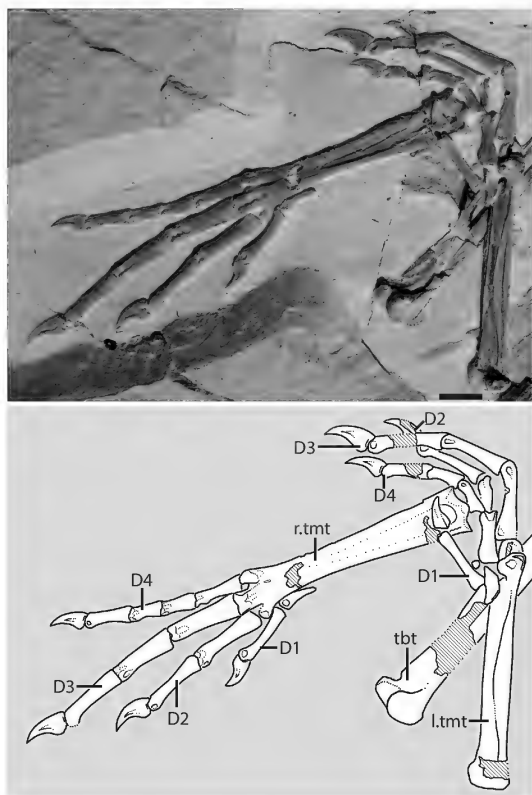


FIG. 19. The hind limbs of FMNH PA 739. The right pes is in anterior/dorsal view whereas the left pes is in medial view. Scale = 1 cm. See anatomical abbreviations.

specimen (Siber and Siber) of *Pseudocrypturus cercanaxius* (table 1). FMNH PA 739 can be assigned only to Lithornithidae at present.

WSGS U1b-2001

Figures 20–22

LOCALITY: Ulrich Quarry within the Fossil Butte Member deposits of the Green River Formation (Locality E of Grande, 2013).

PRESERVATION: This specimen consists of a largely disarticulated skeleton made up of the hind limbs, a partial right forelimb, thoracic ribs, parts of the synsacrum, and ilium, but the skeleton is missing much of the pectoral girdle, the vertebrae, and skull. Some of the bones have deteriorated prior to fossilization (e.g., pelvis,

femur), and segments of some of the bones are missing, but impressions remain (fig. 20).

DESCRIPTION: Of the axial column, only thoracic ribs and part of the synsacrum are preserved. It appears that uncinate processes of the thoracic ribs were unfused to the ribs, but it is possible that they were cartilaginous. The poorly preserved coracoid is possibly the only remnant of the pectoral girdle, but there appears to be a small portion of the furcula near the preserved portion of the coracoid. The coracoid has a narrowly waisted shaft like that of other lithornithids (Houde, 1988). The sternal articulation is restricted to the distal surface, and there does not appear to be any distinct lateral or medial processes. Much of the right humerus is preserved except for the proximal end. The deltopectoral crest is distinctly rounded, and it has a low angle where the crest meets the shaft. The deltopectoral crest appears to be more anterodorsally expanded and proximally restricted in WSGS U1b-2001 than in *Lithornis celestius* (PU 23485), *L. promiscuus* (USNM 336535), and *Paracathartes howardae* (USNM 361420). The shape and size of the crest in WSGS U1b-2001 is similar to that of the Siber and Siber specimen (Houde, 1988: fig. 34) and tinamous, in contrast to other lithornithids (e.g., *Lithornis promiscuus*). Unfortunately, the other Green River Formation specimens are not comparable as the deltopectoral crest is covered or not preserved in all cases. Distally, the m. scapulotriceps groove on the posterior surface is not visible. The dorsal epicondyle and flexor processes are only weakly expanded in this specimen. The humerus is about the same length as the ulna (fig. 20). Most of the ulna and radius are preserved as impressions, and only the distal ends of both elements are preserved, but extensively crushed. The distal end of the radius is rounded, and the distal end of the ulna is compressed and rounded. The shaft of the radius is straight. A complete right ulnare is present, and the dorsal and ventral processes are about the same size. The ventral ramus has a very deep tendinal groove. The midshafts of metacarpals II and III are the only portions pre-

served of the carpometacarpus. Both are straight, and few other details are visible. Impressions of manual phalanges II-1, II-2, and I-2 are present, but uninformative.

The pelvis and the posterior portion of the synsacral vertebrae are poorly preserved. Both femora are present, but these elements are heavily crushed like the pelvic elements. The distal half of the right tibiotarsus lies in anterior view. There is a tendinal groove proximolateral to the medial condyle, and the ossified supratendinal bridge is absent as in other lithornithids, many ratites, and most proximal outgroups to Aves (Clarke, 2004; but see *Iaceornis*). The distal condyles are roughly the same size (fig. 21).

Both pedes are preserved in articulation in dorsal view. The tarsometatarsus bears a short, narrow intercotylar prominence on the proximal surface. Two similarly sized and small proximal vascular foramina occur at the same proximodistal level and lie in a shallow extensor sulcus. Trochlea II is slightly shorter than trochlea IV in distal extent. Metatarsal I is short and lies near the distal end of trochlea II. The phalanges are in articulation. Phalanx I-1 is slightly arched in lateral view (fig. 21). Digit III is the longest, and the phalanges are the most robust relative to the other digits. Like the other Green River Formation lithornithids, the first phalanx is longer than or equally long as any other phalanx in the same digit. The ungual on digit III is the largest, and the other unguals are nearly the same size.

FEATHERING: Feather preservation is exquisite in WSGS U1b-2001. Feather patches are present around the entire specimen, and long feathers of the wing (remiges) diverge from the partially preserved forelimb (fig. 22). The long feathers are generally well preserved and details of individual rachises and barbules are easily discernible. The rachises are preserved with darkened edges and lighter centers. Degradation that must have occurred in early diagenesis is visible in the flight feathers (fig. 22). The feathers are preserved as carbonized traces without textured impressions in the matrix.

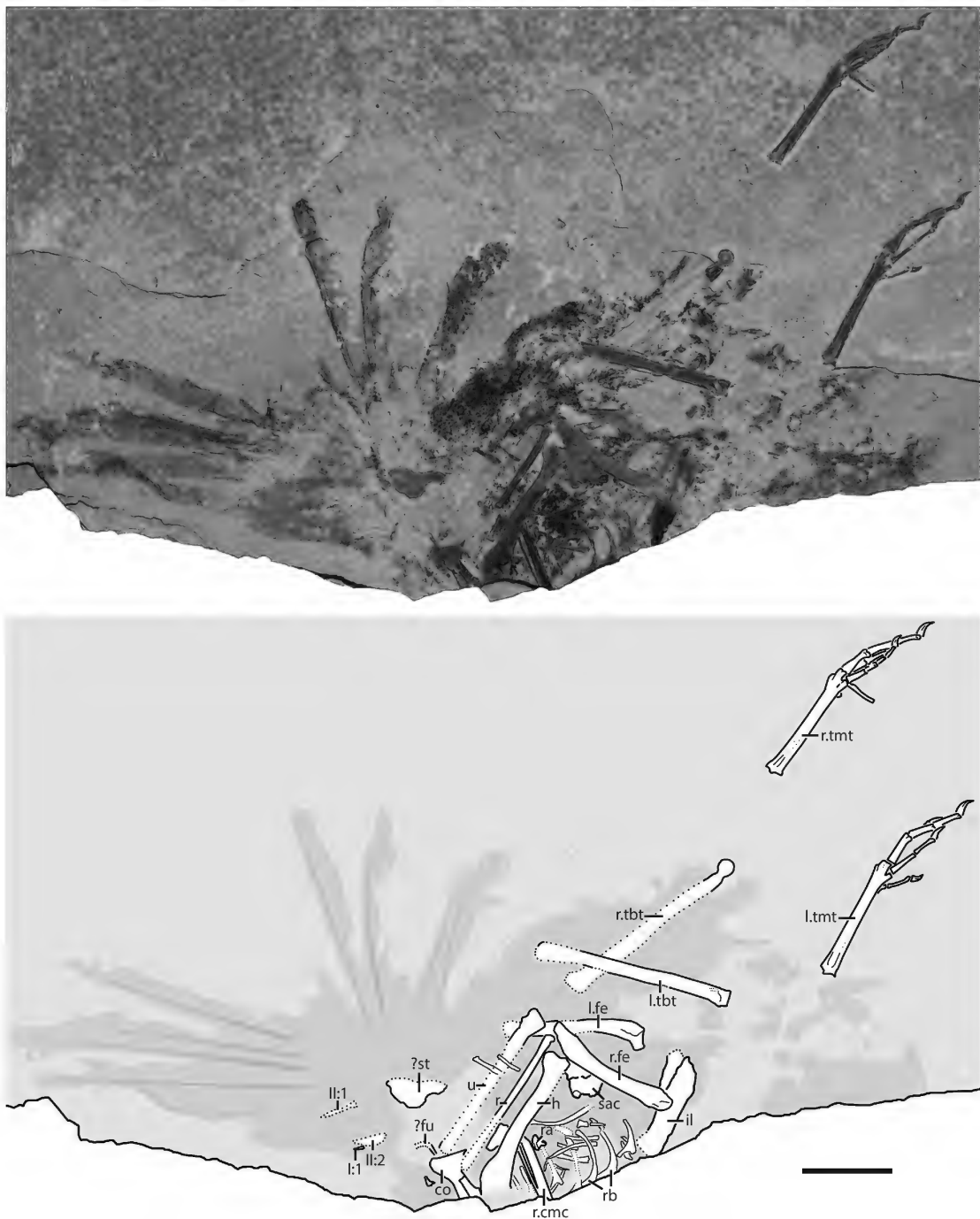


FIG. 20. Skeleton of WGS U1b-2001 (in white) with feather preserved (in dark gray). Scale = 5 cm. See anatomical abbreviations.

PHYLOGENETIC ASSIGNMENT: The assignment of WSGS U1b-2001 to a species-level taxon is difficult given the lack of a skull and other parts of the skeleton. However, the preserved morphology and proportions are consistent with an assignment to Lithornithidae, and this specimen was found within Lithornithidae in our phylogenetic analysis (see below). It lacks an ossified supratendinal bridge (fig. 21). The humerus has a short, rounded deltopectoral crest is similar to that of the Siber and Siber specimen referred to *Pseudocrypturus cercanaxius*. The absolute size and proportions of the limb bones are consistent with the Siber and Siber specimen (= *Pseudocrypturus*) except for the tarsometatarsus, which is ~10% larger than expected as compared to that of the tibiotarsus. Thus, we can refer WSGS U1b-2001 to the Lithornithidae, but do not find support for referral to a more specific taxon within the clade.

PHYLOGENETIC ANALYSIS

TAXON SAMPLING

Our data matrix includes a combination of extinct and extant taxa at the base of Aves (= crown) in order to evaluate the phylogenetic relationships among lithornithids. All extant and extinct taxa, with the exception of parts of the skeleton of *Emeus crassus*, were scored by directed observation. Exemplar species-level taxa for palaeognaths include Dinornithidae (*Emeus crassus*), Struthionidae (*Struthio camelus*), Tinamidae (*Eudromia elegans*, *Crypturellus undulatus*, *Nothura maculosa*, and *Tinamus major*), Apterygidae (*Apteryx owenii*), Rheidae (*Rhea americana*), and the emu (*Dromaeus novaehollandiae*) were used in order to circumvent problems associated with composite higher-level taxa. *Casuarius* was not included; in all recent molecular analyses *Casuarius* has been recovered as the sister taxa of *Dromaius* (e.g., Phillips et al., 2010; Mitchell et al. 2014; Baker et al., 2014). Evaluating the phylogenetic position of elephant birds (Aepyornithidae) was outside the scope of

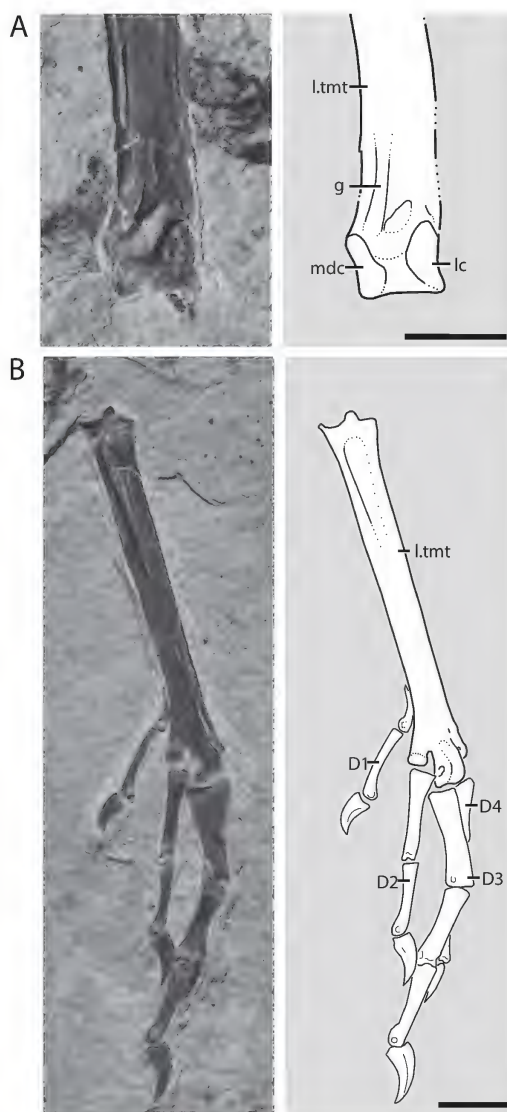


FIG. 21. **A**, Distal end of the left tibiotarsus of WGS U1b-2001 in anterior view. **B**, Complete left pes of WGS U1b-2001 in anterior view. Scales = 1 cm. See anatomical abbreviations.

this analysis, and published illustrations of their anatomy are inconsistent.

Two extant exemplar species were used to represent Galliformes (*Crax pauxi* and *Gallus gallus*), and two to represent Anseriformes (*Anas platyrhynchos* and *Chauna torquata*). *Gavia immer* was included to sample non-Galloanserae



FIG. 22. The well preserved wing feathers of WGS U1b-2001. The white arrows point to the rachis and the black arrow the folding of the feathers. Scale = 1 cm.

neognaths, as the same genus (i.e., *Gavia stellata*) was utilized in the analyses of Phillips et al. (2010). Proposed stem members of crown subclades within Aves (i.e., Struthioniformes, Anatidae) include *Gallinuloides wyomingensis*, *Anatalavis oxfordi*, and *Palaeotis weigelti*. Specimen numbers or literature sources for each taxon are reported in table 2.

Each species-level taxon of lithornithid was scored independently in the phylogenetic analysis (appendix 1). Each specimen was first scored

and then combined into these species-level terminal taxa for the “core” analysis. In the cases of *Lithornis plebius* and *Calciavis grandei*, the scores were based solely on the holotypes (USNM 336534 and AMNH 30578, respectively). For *Lithornis celetius*, the scores were based on the holotype (USNM 290601) and other specimens referred by Houde (1988) from the type locality (USNM 290554, USNM 336200, PU 23483, PU 23484, and PU 23485). The scorings of *Lithornis promiscuus* were based on the holotype (USNM 336535) and a skull (USNM 391983) referred by Houde (1988) found at the same quarry. The scores for *Paracathartes howardae* were based only on referred specimens of a minimum of five individuals (USNM 361402-361446, USNM 391984, USNM 404747-404806; USNM 361415) that were found in the same calcareous nodule (Houde, 1988). The scores of *Pseudocrypturus cercanaxius* derive from the holotype skull (USNM 336103) and a referred specimen (USNM 424078, cast of Siber and Siber lithornithid of Houde, 1988). MGUH 26770, an exquisitely preserved specimen recently referred to *Lithornis vulturinus* (Leonard et al., 2005; Bourdon and Lindow, 2015) was not seen by either of us and, therefore, scored from the description and additional pictures. The specimen was included in the “total analysis” but not the “core lithornithid” analysis because we were unable to confidently score some of the characters. More fragmentary lithornithids were excluded from this analysis because the scorings for those specimens were exactly the same as those for other lithornithid terminal taxa (e.g., *Lithornis vulturinus*, *Lithornis nasi*).

Outgroup selection for analyses of Aves remains an outstanding problem in investigations of avian relationships because of highly incomplete skeletons and specialized ecologies (e.g., full aquatic). Here, we used *Apsaravis ukhaana* Norell and Clarke, 2001, and *Ichthyornis dispar* Marsh, 1872 (sensu Clarke, 2004), as outgroups. *Apsaravis ukhaana* and *Ichthyornis dispar* have been found outside Aves in many phylogenetic analyses of avialan relationships

TABLE 2
Specimens and literature sources for the scoring of taxa in the phylogenetic analysis
See institutional abbreviations.

Taxon	Source
<i>Anas platyrhynchos</i>	TMM M-4829
<i>Anatalavis oxfordi</i>	NHMUK A5922; Olson, 1999
<i>Apsaravis ukhaana</i>	IGM 100/1017, Norell and Clarke, 2001; Clarke and Norell, 2002
<i>Apteryx owenii</i>	USNM 18279
<i>Calciavis grandei</i>	AMNH 30578, AMNH 30560
<i>Chauna torquata</i>	AMNH 1773
<i>Crax pauxi</i>	AMNH 4719
<i>Crypturellus undulatus</i>	AMNH 6480
<i>Dromaius novaehollandiae</i>	mounted skeleton TMM, unnumbered
<i>Eudromia elegans</i>	USNM 345096
<i>Emeus crassus</i>	FMNH specimens, Parker, 1895; Worthy and Holdaway, 2002
<i>Gallinuloides wyomingensis</i>	MCZ 342221, WDC CGR-012
<i>Gallus gallus</i>	USNM 19369
<i>Gavia immer</i>	TMM, unnumbered
<i>Ichthyornis dispar</i>	specimens listed by Clarke, 2004
<i>Lithornis celetius</i>	USNM 290601, USNM 290554, USNM 336200, PU 23483, PU 23484, PU 23485
<i>Lithornis plebius</i>	USNM 336534
<i>Lithornis promiscuus</i>	USNM 336535, USNM 391983
<i>Lithornis vulturinus</i>	MGUH 26770, Leonard et al., 2005; Bourdon and Lindow, 2015
<i>Nothura maculosa</i>	USNM 614501
<i>Palaeotis weigelti</i>	GM 4362; HLMD Me 7530 (casts at USNM); Houde and Haubold, 1987; Mayr, 2015
<i>Paracathartes howardae</i>	Specimens listed in Houde, 1988
<i>Pseudocrypturus cercanaxius</i>	USNM 336103, USNM 424078 (cast of Siber and Siber specimen)
<i>Rhea americana</i>	USNM 555661, USNM 428554, TMM M-4938
<i>Struthio camelus</i>	USNM 560081, USNM 346697, USNM 224856
<i>Tinamus major</i>	USNM 621693

(e.g., Chiappe, 2002; Clarke and Norell, 2002; Clarke, 2004; Clarke et al., 2006; You et al., 2006).

CHARACTER SAMPLING

The data matrix consists of 182 morphological characters scored for 38 terminal taxa. Of the orig-

inal 182 characters, 18 were found as parsimony uninformative in the total analysis, and 20 characters were found as parsimony uninformative in the “core lithornithid” analysis. The parsimony-uninformative characters were kept in the data set to facilitate future expansion of character and taxonomic sampling, given that the parsimony-unin-

formative characters found here have supported clades in previous analyses (e.g., Clarke, 2004; Clarke et al., 2006). Characters 20, 25, 57, 59, 65, 68, 69, 70, 81, 83, 86, 104, 107, 118, 119, 137, 140, 154, 166, 168, 173, and 178 were ordered according to previous usage of the characters in other data sets and evidence of nested morphologies (Slowinski, 1993) for new characters. Our matrix combines characters from the morphological data sets of Cracraft (1974), Bledsoe (1988), Lee et al. (1997); Mayr and Clarke (2003), Clarke (2004), and Clarke et al. (2006) and new observations by the authors. The Bourdon et al. (2009) character set (128 characters) unfortunately included many composite character states (referencing multiple morphologies in one character set up as a binary with no description of the plesiomorphic state, e.g., “Ossa digiti IV, phalanges proximales et intermedia gradually shortening toward phalanx ungualis, so that phalanx intermedia just proximal to the latter is either wider than long or nearly square in shape: no (0); yes (1)”; Bourdon et al., 2009: 63, char. 126) that made it difficult to assimilate directly with other previously described characters. Many of these characters also were based on previous data sets (e.g., Cracraft, 1974; Bledsoe, 1988; Lee et al., 1997) that were considered at the time of data set construction. Another more recently published character (Worthy and Scofield, 2012, utilized in Mitchell et al., 2014; 179 characters) drew on many of these previous sets, especially revising Bourdon et al. (2009). This data set recovered a supraspecific lithornithid terminal taxon in an unresolved polytomy with the rest of Palaeognathae. Here, we were focused on adding characters relevant to relationships among lithornithids and consider our data set to address distinct aims from the valuable Worthy and Scofield (2012) data set. Future detailed work assimilating all of these character sets is clearly necessary.

Character descriptions are included below with character citations and modifications. The most recent author to use previously modified characters is cited in the character list; citations of the previous usage of the characters is not meant to be exhaustive (appendix 1).

METHODS

The character-taxon matrix was assembled in Morphobank (O’Leary and Kaufman, 2012) and is published under project 340. We analyzed our data set using PAUP* 4.0b10 for Macintosh PPC (Swofford, 2002). Trees were searched for using the parsimony criterion implemented under the heuristic search option using tree bisection and reconnection (TBR) with 1000 random-addition sequence replicates. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. All characters were equally weighted. Bootstrap support was calculated from 1000 replicates using a heuristic search strategy with random taxon addition sequence and TBR branch swapping (Efron, 1979; Felsenstein, 1985). Bremer support was calculated manually in PAUP*4.0b10. Multistate scorings for terminals indicate polymorphism, which is treated as a “?” in our analysis.

We conducted two phylogenetic analyses without constraint trees that differed only by the inclusion of lithornithid taxa. In the “total” analysis, we included all lithornithids individuals as separate terminal taxa. For example, each Green River Formation lithornithid was its own terminal taxon (e.g., AMNH 30560), and the two specimens of *Lithornis promiscuus* were scored separately as the “*Lithornis promiscuus* holotype” (USNM 336535) and a referred skull (USNM 391983) as “*Lithornis promiscuus* skull.” We utilized this conservative strategy because: (1) the referral of some specimens to Lithornithidae is not always clear because of the lack of clearly defined apomorphies; and (2) the referral of some specimens to species-level lithornithid taxa from the same locality or same geological unit is not clear especially when there are few overlapping skeletal elements.

In the “core lithornithid” analysis, the number of terminal taxa was reduced to 25 taxa because we combined individual lithornithid specimens into species-level terminal taxa (labeled as “combined”). Specimens were combined in species-level terminal taxa after rediagnosing each of the

lithornithid taxa utilized in this analysis (see appendix 2). In these cases, the individual specimens of lithornithids were almost always from the same locality and always from the same geological unit (see Houde, 1988).

Following the initial run of data set, we built various constraint trees for palaeognath relationships using the “core lithornithid” taxon sampling to explore the effect of alternative previously hypothesized topologies on the relationships among lithornithids. Further, we used these constraint trees to examine the effects on character support for Aves, Palaeognathae, and Lithornithidae (Houde, 1988; Dyke, 2003; Clarke, 2004; Livezey and Zusi, 2006, 2007; Leonard et al., 2005; Phillips et al., 2010; Johnston, 2011; Mitchell et al., 2014; Baker et al., 2014). Constraint trees were built in McClade (version 4.08; Maddison and Maddison, 2005) and then imported into PAUP. The constraint trees were loaded and then the option “enforce topological constraints” was chosen under the heuristic search settings. The proceeding analysis was then run as described above for the unconstrained analyses.

RESULTS

In both unconstrained analyses, we recovered the Neognathae-Palaeognathae split at the base of Aves (figs. 23, 24) as previously recovered in morphological and molecular studies of avian relationships (e.g., Cracraft, 1988; Mayr and Clarke, 2003; Van Tuinen et al., 2000; Livezey and Zusi, 2006, 2007; Hackett et al., 2008; Jarvis et al., 2014). *Ichthyornis dispar* was found as the sister taxon of Aves as in all recent phylogenetic analyses of early diverging avian relationships. The relationships of neognaths are similar to those of morphological (Clarke, 2004; Livezey and Zusi, 2006, 2007) and recent molecular analyses (Hackett et al., 2008; Jarvis et al., 2014), whereas the palaeognath relationships are similar to those of the morphology-only phylogenetic hypotheses of Lee et al. (1997) and Bourdon et al. (2009). In contrast to nearly all molecular hypotheses that find *Apteryx* as the sister taxon

to a *Casuarius-Dromaeus* clade (Lee et al., 1997; Cooper et al., 2001; Hackett et al., 2008; Phillips et al., 2010; Baker et al., 2014), we recover *Apteryx* as the sister taxon to the moa *Emeus crassus* at the base of ratites similar to the results in Cracraft (1974). *Palaeotis weigelti* was found outside a *Struthio* + *Dromaius* + *Rhea* clade. This result is identical to that of recent analysis of *Palaeotis weigelti* from an entirely different data set with similar taxon sampling (Mayr, 2015).

In both the “total” (fig. 23) and “core lithornithid” (fig. 24) analyses, we recovered a monophyletic Lithornithidae as the sister taxon of Tinamidae at the base of Palaeognathae. In both analyses, tinamous collapsed into a polytomy in the consensus tree. In the “total” analysis (tree length [TL] = 470; most parsimonious trees [MPTs] = 2724; consistency index [CI] = 0.452; retention index [RI] = 0.691; recalculated consistency index [RC] = 0.312), all of the taxa or specimens previously hypothesized to belong to Lithornithidae were found in a monophyletic group. All the lithornithids collapsed into a polytomy without any ingroup resolution in the strict consensus tree (fig. 23). The monophyly of Lithornithidae is supported by a combination of the following unambiguous character states (some of which represent the same states, presumably plesiomorphic states, present in out-group taxa (= *)): quadrate with a small fossae on the posterior side of the body (C38:1); orbital process of the quadrate short, hatchet shaped, significantly shorter than the length of the body (C41:1*); centrally located ovoid foramina lateral surfaces of centra of the thoracic vertebrae (C67:2*); only three sacral vertebrae with dorsally directed parapophyses just anterior to the acetabulum (C70:1*); foramina present posteroventral surface to the hooked acrocoracoid process of the coracoid (C95:1); acromion of the scapula laterally hooked tip with small foramina on the posterior side (C104:2); tubercle present where this ramus joins the dorsal margin of the ulnare (C133:1); infratrochlearis fossa deeply excavating the proximal surface of the pisiform process on the

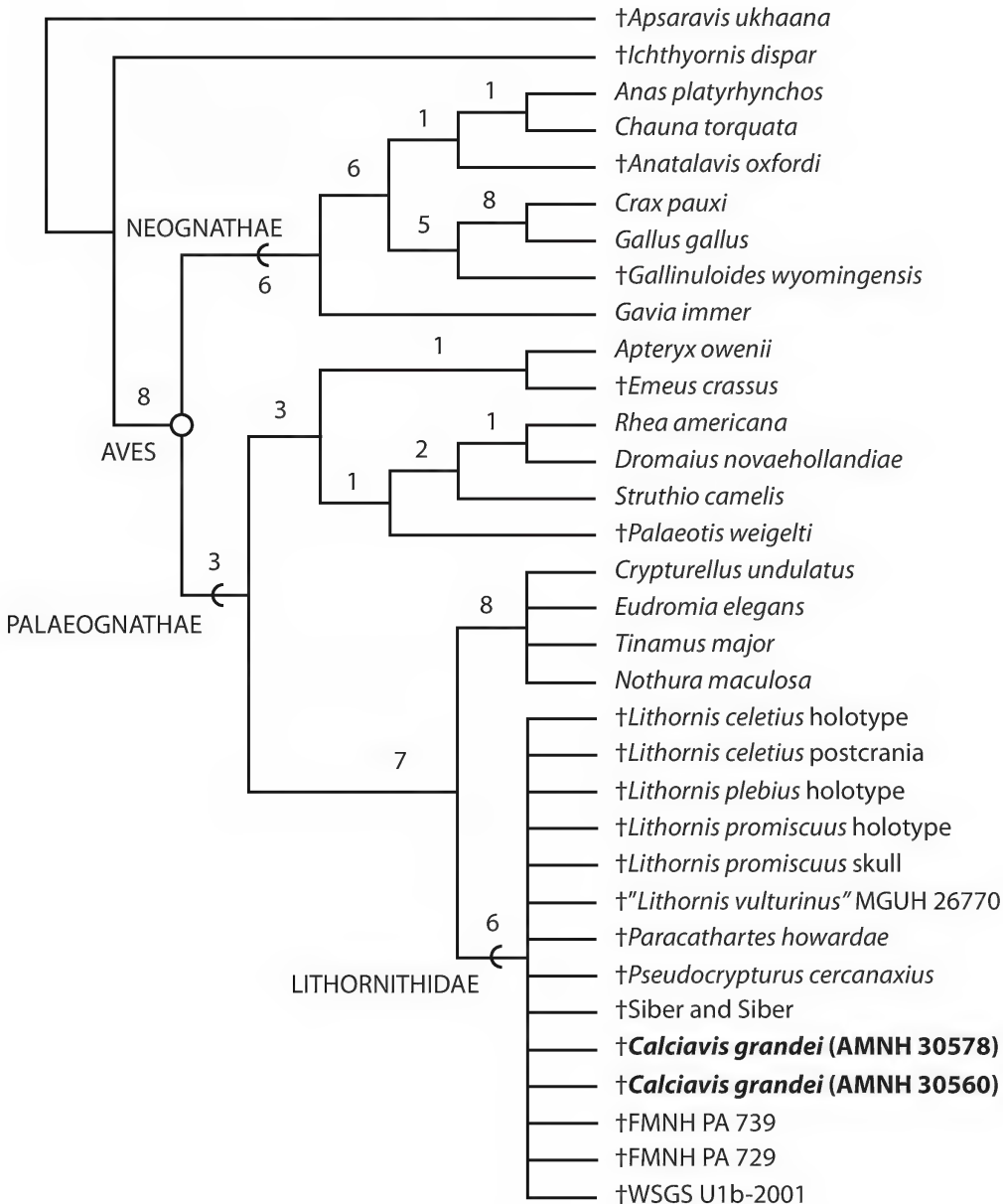


FIG. 23. Strict consensus (TL = 470; MPTs = 2724; CI = 0.452; RI = 0.691; RC = 0.312) of the "total" analysis. Bremer supports located above branches.

ventral surface of the carpometacarpus (C136:1); deep groove at the distal end of the posterior side of the carpal trochlea of the proximal portion of the carpometacarpus (C138:1); and distinct tuber present on the ventral side of the proximal portion of metacarpal III (C143:1).

Our "core lithornithid" analysis (TL = 470; MPTs = 29; CI = 0.451; RI = 0.676; RC = 0.305) recovered a monophyletic Lithornithidae. However, all lithornithid taxa collapsed into a polytomy with no ingroup resolution in the strict consensus. The monophyly of Lithornithidae is

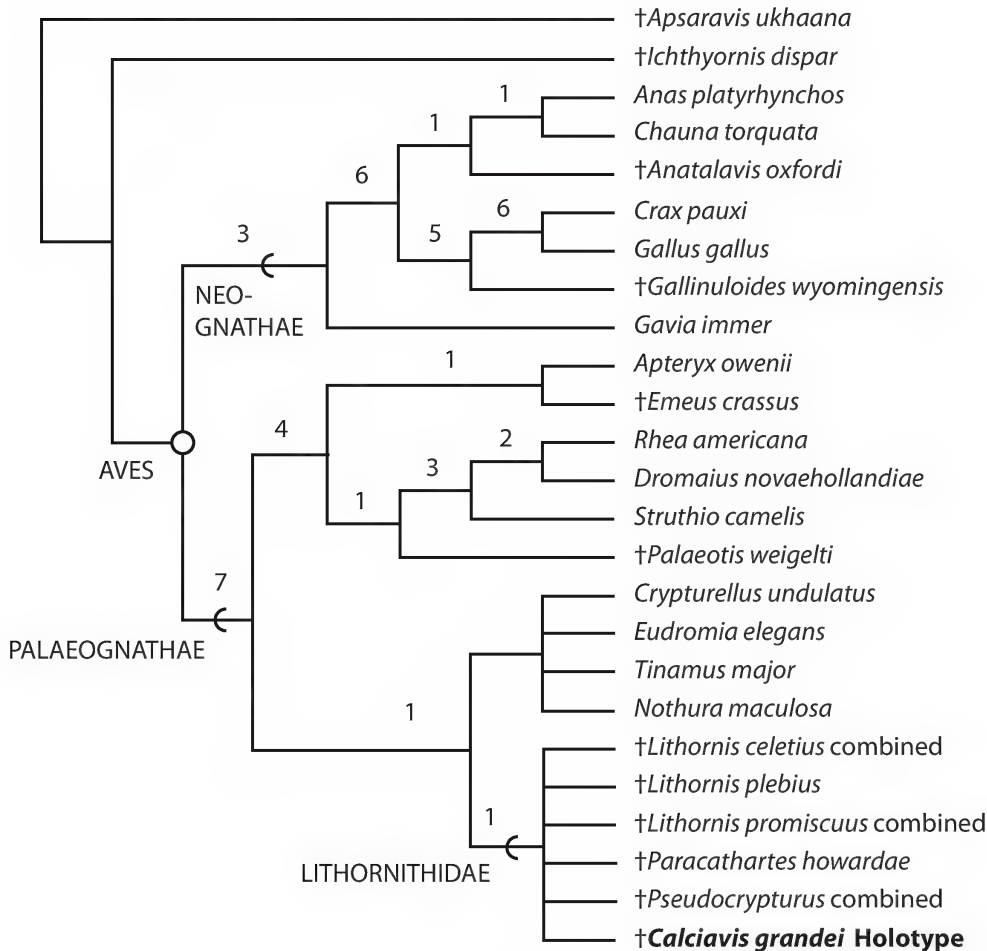


FIG. 24. Strict consensus (TL = 470; MPTs = 29; CI = 0.451; RI = 0.676; RC = 0.305) of the "core lithornithid" analysis. Bremer supports located above branches.

supported by a combination of the following unambiguous character states: broad, flat ventral process of the lacrimal in lateral view (C13:1); quadrate with a small fossae on the posterior side of the body (C38:1*); orbital process of the quadrate short, hatchet shaped, significantly shorter than the length of the body (C41:1); short finger-like retroarticular process just posterior to the articular facets of the mandible (C60:1); in the third cervical vertebra, the presence of an osseous bridge from the transverse process to the postzygapophysis so a foramen is formed in dorsal view (C64:1); centrally located ovoid foramina on the lateral surfaces of the centra of the

thoracic vertebrae (C67:2*); number of ankylosed synsacral vertebrae numbering 11–14 (C69:1); three synsacral vertebrae with dorsally directed transverse processes in the area of the acetabulum (C70:1*); coracoidal sulci spacing on anterior edge of the sternum crossed on midline (C79:1); absence of trabeculae on the posterior margin of the sternum (C83:0); foramina present on the posteroventral surface of the hooked acrocoracoid process of the coracoid (C95:1); acromion of the scapula laterally hooked tip with small foramina on the posterior side (C104:2); infratrochlear fossa deeply excavating the proximal surface of the pisiform process on the ven-

tral surface of the carpometacarpus (C136:1); distinct tuber present on the ventral side of the proximal portion of metacarpal III (C143:1).

Within Lithornithidae, the interrelationships were completely unresolved in both analyses. However, there are a number of lithornithids that were closely related in the most of the MPTs, but these relationships are no better supported than others found in various MPTs. *Calciavis grandei* and *Pseudocrypturus cercanaxius* were almost always closely related in two positions: (1) as sister taxa as the most nested lithornithids; or (2) in a hard polytomy at the base of with each other and all other Lithornithidae. The sister-taxon relationship well nested in Lithornithidae is supported by two unambiguous character states in both analyses: anteroposterior straight medial margin of the pterygoid anterior to the articulation the basipterygoid process (C22:0) and distal extent of trochlea II and trochlea IV equal (C180:0). In this phylogenetic position, these two character states optimize as independently derived from the plesiomorphic condition found outside Lithornithidae among basal palaeognaths. In contrast, the same two character states represent plesiomorphies at Lithornithidae + Tinamidae and keep *Calciavis grandei* and *Pseudocrypturus cercanaxius* at the base of Lithornithidae. The other couplet typically found in most MPTs is a sister-taxon relationship between *Paracathartes howardae* and *Lithornis promiscuus*. This clade is found in nearly all positions among other lithornithids and is always supported by the height of shaft at the proximal end of the scapula greater than the height of the humeral glenoid (C105:1).

In the "total" unconstrained analysis, a Lithornithidae-Tinamidae clade is supported by the following unambiguous character states: maxillopalatine antrum absent (C4:0); frontal-parietal suture open (C12:0); extensive contact between the lacrimal and ectethmoid (C16:1); cluster of pneumatic foramina on the posterior surface of the otic head of the quadrate (C43:1); small horizontal shelf at the posterior portion of the mandibular symphysis (C48:1); corpus of the axis with pneumatic foramina on lateral sides (C62:1);

acromion of the scapula projected anteriorly to surpass the articular surface for coracoid (tuberculum coracoidei of Baumel and Witmer, 1993) of the scapula (C103:0); pneumatic foramina within of pneumotricipital fossa of the humerus (C111:1); intermetacarpal space (between metacarpals II and III) terminates distal to end of metacarpal I (C141:1); manual digit III, phalanx 1, length less than 50% the length of digit II, phalanx 1 (C146:1); plantar surface of the tarsometatarsus trochlea II and IV expanded into distinct "wings" (C177:1). The character support for the Lithornithidae-Tinamidae clade in the "core lithornithid" analysis was nearly identical to that of the "total" analysis except that character state (C43:1) did not diagnose the clade in the "core lithornithid" analysis.

"Core lithornithid" analysis (fig. 24)

CONSTRAINT: None.

SUPPORT: Aves – C66:1, C69:2, C70:2, C71:1, C93:1, C102:0, C113:1, C114:0, C115:0, C117:1, C118:2, C129:0, C149:1, C165:0; Palaeognathae – C5:1, C9:1, C31:1, C36:0, C42:0, C51:1, C72:1, C137:1, C167:1, C180:0; Lithornithidae – C13:1, C38:1, C41:1, C60:1, C67:2, C69:1, C70:1, C79:1, C83:0, C95:1, C104:2, C136:1, C143:1.

CONSTRAINT TREES AND ALTERNATE HYPOTHESES OF THE RELATIONSHIPS OF LITHORNITHIDAE

The impact on the inferred relationships among Lithornithidae species of imposing constraint trees to reflect: (1) previously proposed hypotheses of their relationships among basal avians (table 3); and (2) phylogenetic results from large-scale molecular sequence based analyses of Aves were explored. Constraint trees enforced placement of Lithornithidae as the sister taxon of Aves following Livezey and Zusi (2006; 2007), as a non-monophyletic group where *Paracathartes* was closer to ratites than other lithornithids following Houde (1986; 1988), and as the sister taxon to all other Palaeognathae or of ratites (Clarke, 2004).

TABLE 3
Constraint tree statistics compared

Constraint	# of trees	Tree Length	CI	RI	RC
none	29	470	0.451	0.676	0.305
Lithornithidae as the sister taxon of Aves	10	+10	0.442	0.664	0.293
Lithornithidae as the sister taxon of all other Palaeognathae	6	+8	0.44	0.666	0.295
Lithornithidae as the sister taxon of ratites	7	+11	0.441	0.662	0.292
Non-monophyletic Lithornithidae where <i>Paracathartes</i> as the sister taxon of ratites	4	+17	0.435	0.655	0.285
Palaeognathae relationships from molecular analyses of Phillips et al. (2010)	4	+41	0.415	0.625	0.259
Palaeognathae relationships from molecular analyses of Baker et al. (2014)	8	+38	0.415	0.628	0.261
Palaeognathae relationships from molecular analyses of Mitchell et al. (2014)	8	+30	0.420	0.624	0.262

We also explored the affect on the inferred relationships of Lithornithidae of constraining the relationships of extant Palaeognathae to match the phylogenetic results obtained from diverse large molecular data sets by Phillips et al. (2010), Baker et al. (2014), and Mitchell et al. (2014). The relationships recovered in the “total” analysis described above are at odds with all recent molecular analyses of avian relationships (Harshman et al., 2008; Phillips et al., 2010; Smith et al., 2013a; Haddrath and Baker, 2012; Baker et al., 2014; Mitchell et al., 2014; Jarvis et al., 2014).

In the sections below, we present how the taxa were constrained, the resultant tree (figs. 25–31), tree statistics (table 3), and character support for recovered clades. The Tinamidae + Lithornithidae clade (fig. 23) is not recovered in these analyses with the exception of a constraint placing *Paracathartes* as the sister taxon of a monophyletic Ratitae (Houde, 1988).

Constraints based on previously proposed placements of the Lithornithidae

Lithornithidae as the sister taxon of Aves (fig. 25)

CONSTRAINT: Lithornithidae was constrained as the monophyletic sister taxon of all

members of Aves found in the “core lithornithid” tree (fig. 24). All other taxa were unconstrained, and lithornithid interrelationships were unconstrained.

SUPPORT: Lithornithidae + Aves – C51:1, C66:1, C71:1, C93:1, C110:1, C113:1, C114:0, C115:0, C118:2, C129:0, C137:1, C140:2, C149:1, C165:0, C167:1, C181:1; Aves – C69:2, C70:2, C99:1, C117:1, C129:0, C136:0, C166:2; Lithornithidae – C13:1, C60:1, C64:1, C67:2, C83:0, C95:1, C104:2, C112:0, C143:1.

RESULTS: With Lithornithidae outside Aves, Tinamidae was found as the sister taxon of Palaeognathae + Neognathae. Therefore, Palaeognathae did not include Tinamidae, and *Emeus crassus* + *Apteryx owenii* are the earliest diverging members of the clade. The relationships of Lithornithidae are fully resolved, but anseriform taxa form a polytomy. Within Lithornithidae, *Lithornis* is paraphyletic and the two Green River Formation taxa are sister taxa and well nested within the clade. At the base of Lithornithidae, *Lithornis celetius* shares a number of character states (e.g., elongated pectineal process of the pubis) with the tinamou clade, and thus these character states optimize as plesiomorphic for Aves. All other relationships were the same as the “core lithornithid” analysis.

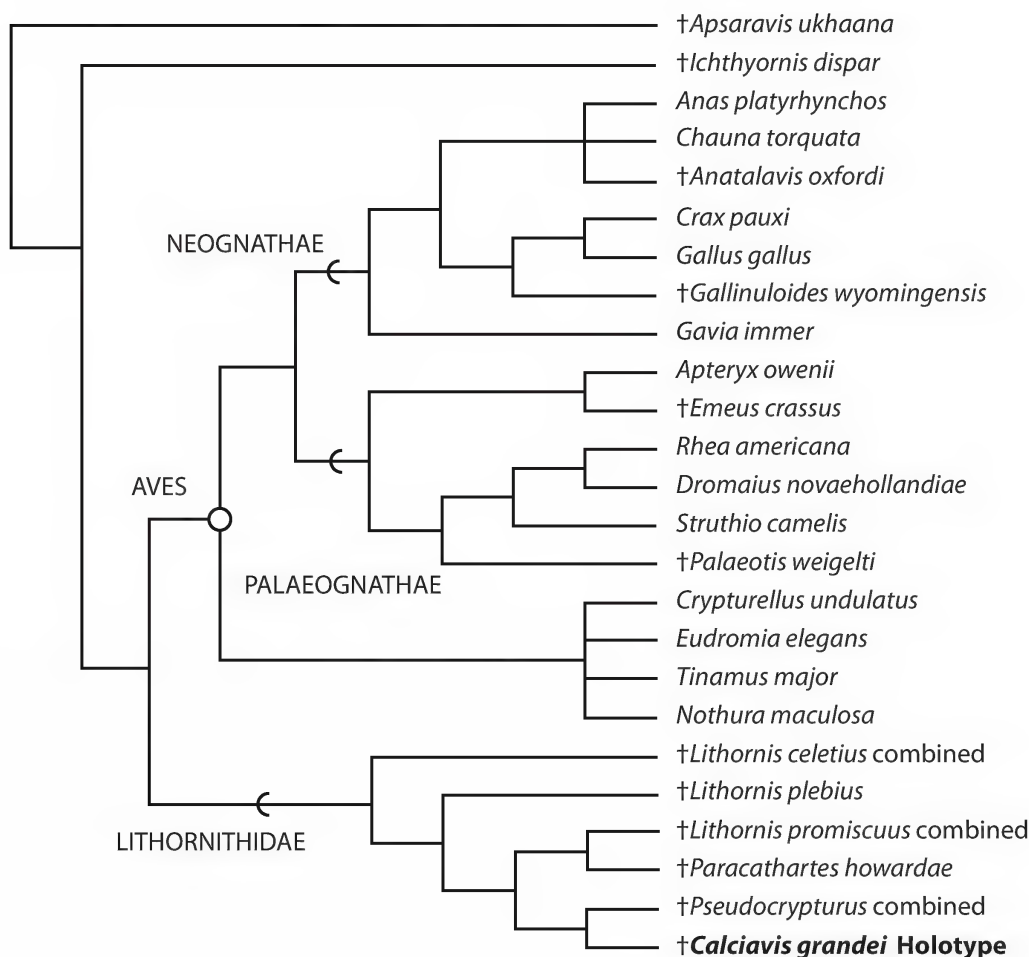


FIG. 25. Strict consensus when Lithornithidae is constrained as the sister taxon of Aves.

Lithornithidae as the sister taxon of all other Palaeognathae (fig. 26)

CONSTRAINT: Lithornithidae was constrained as a monophyletic group (but interrelationships were unconstrained) as the sister taxon of all members of Palaeognathae found in the “core lithornithid” tree. All other taxa were unconstrained.

SUPPORT: Aves – C66:1, C71:1, C93:1, C102:0, C110:1, C113:1, C114:0, C115:0, C117:1, C118:2, C129:0, C149:1, C165:0, and C181:1; Palaeognathae – C5:1, C9:1, C31:1, C36:0, C42:0, C51:1, C135:1, C137:1, C139:1, and C167:1; Lithornithi-

dae – C13:1, C38:1, C41:1, C60:1, C64:1, C67:2, C79:1, C83:0, C95:1, C104:2, C112:0, C136:1, and C143:1.

RESULTS: With Lithornithidae constrained as the sister taxon of all other Palaeognathae, the Lithornithidae + Tinamou clade is no longer recovered; tinamous are the sister taxon of all ratites. Within a nearly unresolved Lithornithidae, *Lithornis promiscuus* and *Paracathartes howardae* were found as sister taxa. The relationships of the three anseriforms dissolved into a polytomy. All other relationships were the same as the “core lithornithid” analysis.

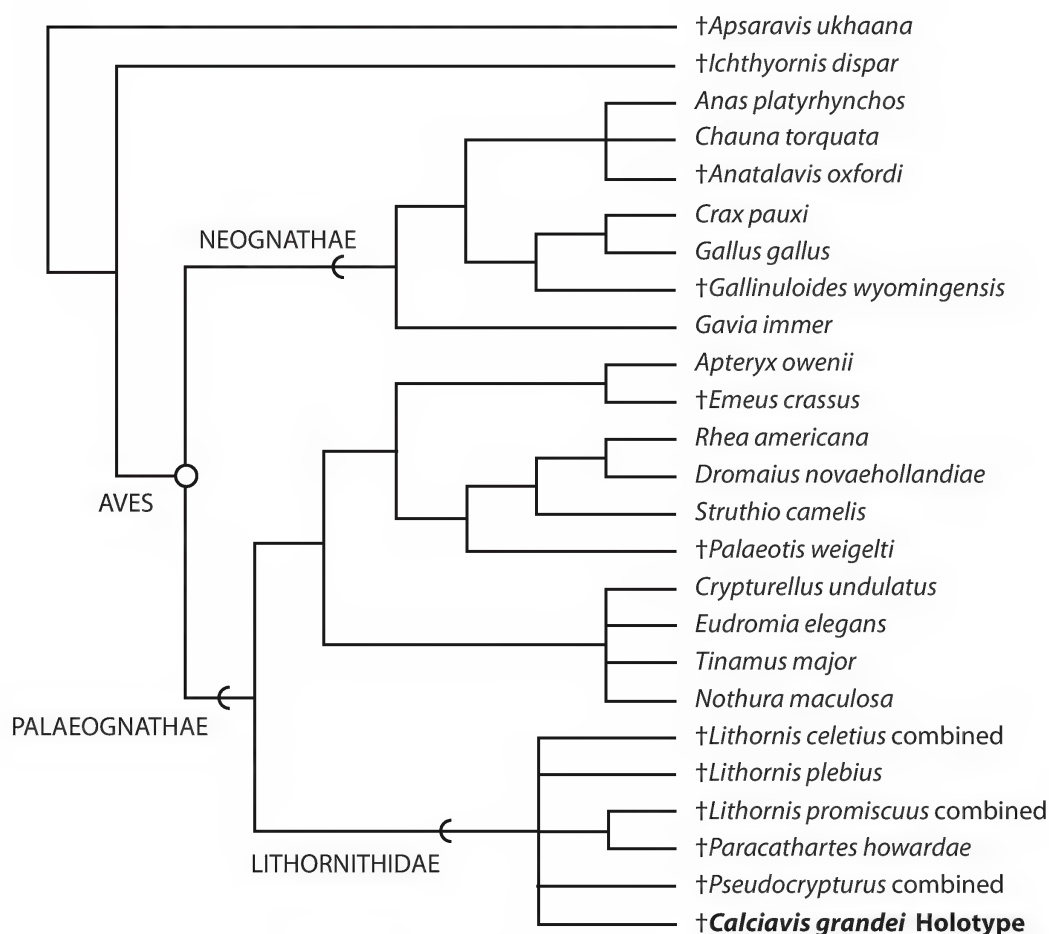


FIG. 26. Strict consensus when Lithornithidae is constrained as the sister taxon of all other Palaeognathae.

Lithornithidae as the sister taxon of ratites (fig. 27)

CONSTRAINT: Lithornithidae was constrained as the monophyletic sister taxon of all flightless ratites found in the “core lithornithid” tree. All other taxa unconstrained.

SUPPORT: Aves – C66:1, C69:2, C70:2, C71:1, C93:1, C110:1, C113:1, C114:0, C115:0, C117:1, C118:2, C129:0, C149:1, C165:0, and C181:1; Palaeognathae – C5:1, C9:1, C31:1, C36:0, C42:0, C51:1, C72:1, C135:1, C137:1, C139:1, C154:2, and C167:1; Lithornithidae + Ratites - None

Lithornithidae – C60:1, C67:2, C69:1, C70:1, C79:1, C83:0, C104:2, C112:0, and C143:1.

RESULTS: With Lithornithidae constrained as the sister taxon of all ratites, there is very little effect on recovered relationships. However, a Lithornithidae + tinamou clade is no longer recovered. Species relationships in Lithornithidae are nearly completely resolved, and those in Tinamidae are completely unresolved. *Lithornis* is again paraphyletic and the Green River Formation lithornithids are again recovered as sister taxa.

Lithornithid *Paracathartes howardae* as the sister taxon to all crown ratites (fig. 28)

CONSTRAINT: *Paracathartes howardae* was constrained as the sister taxon of all crown ratites

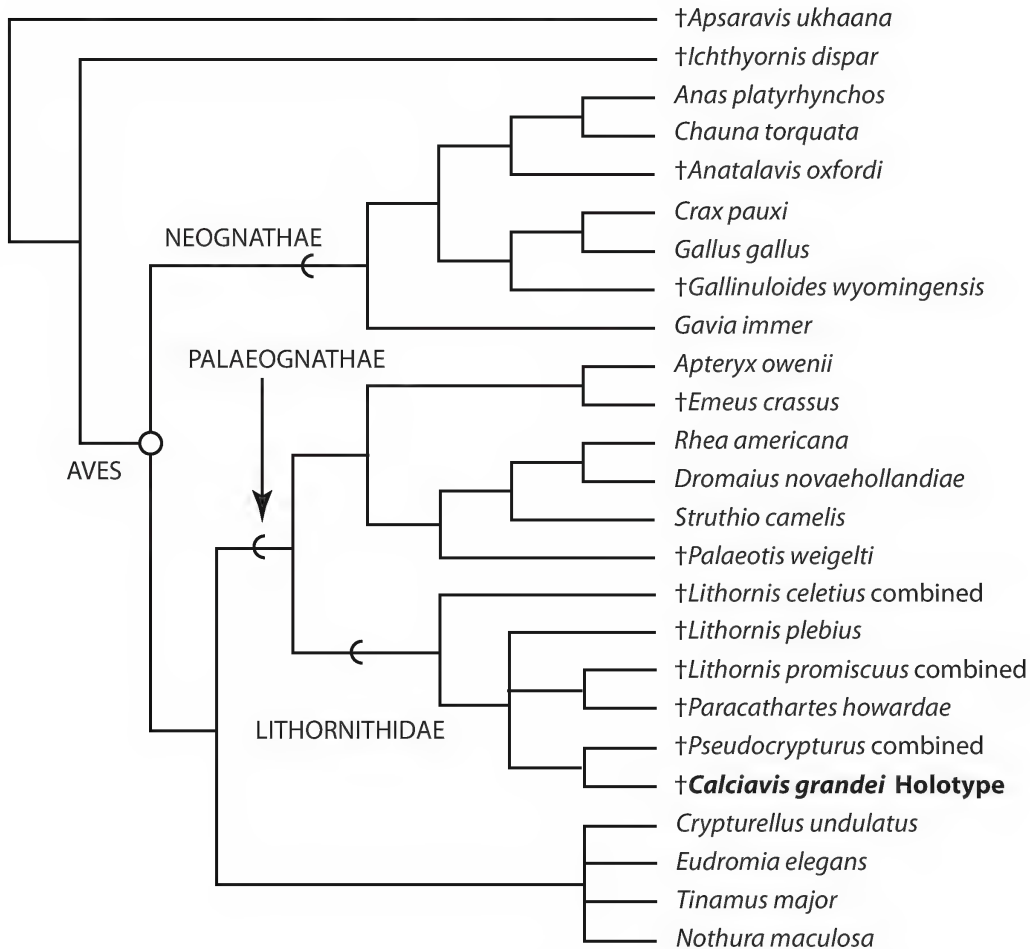


FIG. 27. Strict consensus when Lithornithidae is constrained as the sister taxon of ratites.

(one of the hypotheses of Houde, 1988). All other taxa were unconstrained.

SUPPORT: Aves – C66:1, C69:2, C70:2, C71:1, C93:1, C102:0, C110:1, C113:1, C114:0, C115:0, C117:1, C118:2, C129:1, C149:1, C165:0, and C181:1; Palaeognathae – C5:1, C9:1, C31:1, C36:0, C42:0, C51:1, C72:1, C135:1, and C167:1; Lithornithidae [no *Paracathartes howardae*] – C4:0, C16:1, C111:1, C146:1, and C150:1. *Paracathartes howardae* + Ratites – C17:1.

RESULTS: The relationships of the included Aves are nearly identical to that of the unconstrained analysis. All lithornithids except *Paracathartes howardae* were found in a clade as the sister taxon of Tinamidae. The interrelationships of Lithornithidae are completely resolved. *Lithornis* is recovered as

monophyletic in this analysis, and the Green River Formation species are again sister taxa.

Constraints based on large-scale molecular phylogenies

Palaeognath relationships from Phillips et al. (2010) (fig. 29)

CONSTRAINT: Palaeognath relationships were constrained (as a backbone constraint in PAUP) to match the taxon sampling and results of Phillips et al. (2010). All other taxa were unconstrained.

SUPPORT: Aves – C66:1, C71:1, C93:1, C102:0, C113:1, C114:0, C115:0, C117:1, C118:2, C129:0, and C149:1; Palaeognathae – C5:1, C9:1, C31:1,

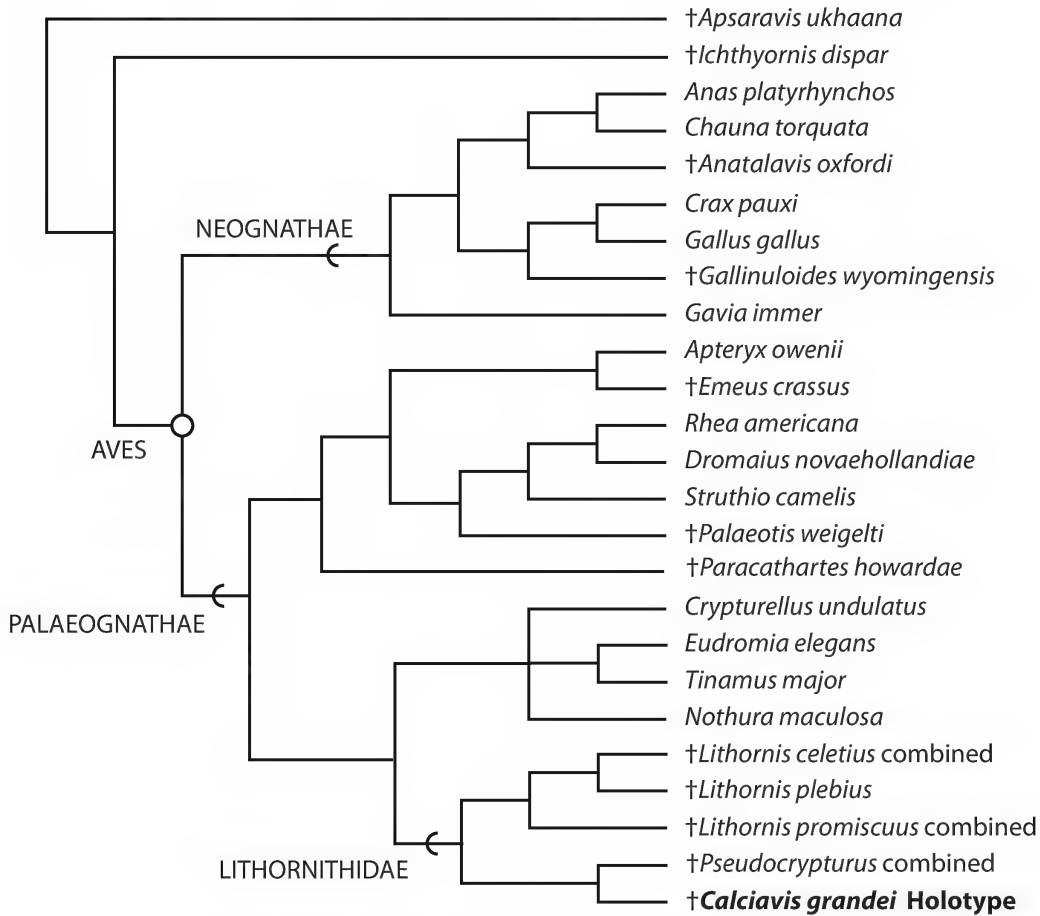


FIG. 28. Strict consensus when Lithornithidae is constrained as not monophyletic and *Paracathartes howardae* is the sister taxon to all extant ratites.

C36:0, C42:0, C51:1, C72:1, C137:1, C139:1, C167:1, and C180:0; Lithornithidae – C4:0, C12:0, C16:1, C20:2, C60:1, C64:1, C67:2, C83:0, C103:0, C104:2, C112:0, C133:1, C141:1, C143:1, C150:1, and C177:1.

RESULTS: Constraining the relationships among Palaeognathae to those recovered by Phillips et al. (2010) results in Lithornithidae being recovered as the basalmost clade of Palaeognathae and not as the sister taxon of Tinamidae. Tinamidae are highly nested within the clade (Phillips et al., 2010). The extinct *Palaeotis weigelti* was found as the sister taxon of extant palaeognaths. The interrelationships within Tinamidae are fully resolved, some of the interrelationships of lithornithids were resolved, and the

interrelationships of the included anseriforms were unresolved. A monophyletic *Lithornis* + *Paracathartes* clade is recovered but the Green River Formation lithornithid species are not recovered as sister taxa.

Palaeognath relationships of from Baker et al. (2014: figure 3) (fig. 30)

CONSTRAINT: Palaeognath relationships were constrained (as a backbone constraint in PAUP) to match figure 3 of Baker et al. (2014). This is the tree of Haddrath and Baker (2012; based on 27 nuclear genes and 21 retroelements) with eight novel retroelement insertions mapped; Baker et al., 2014). All other taxa were unconstrained.

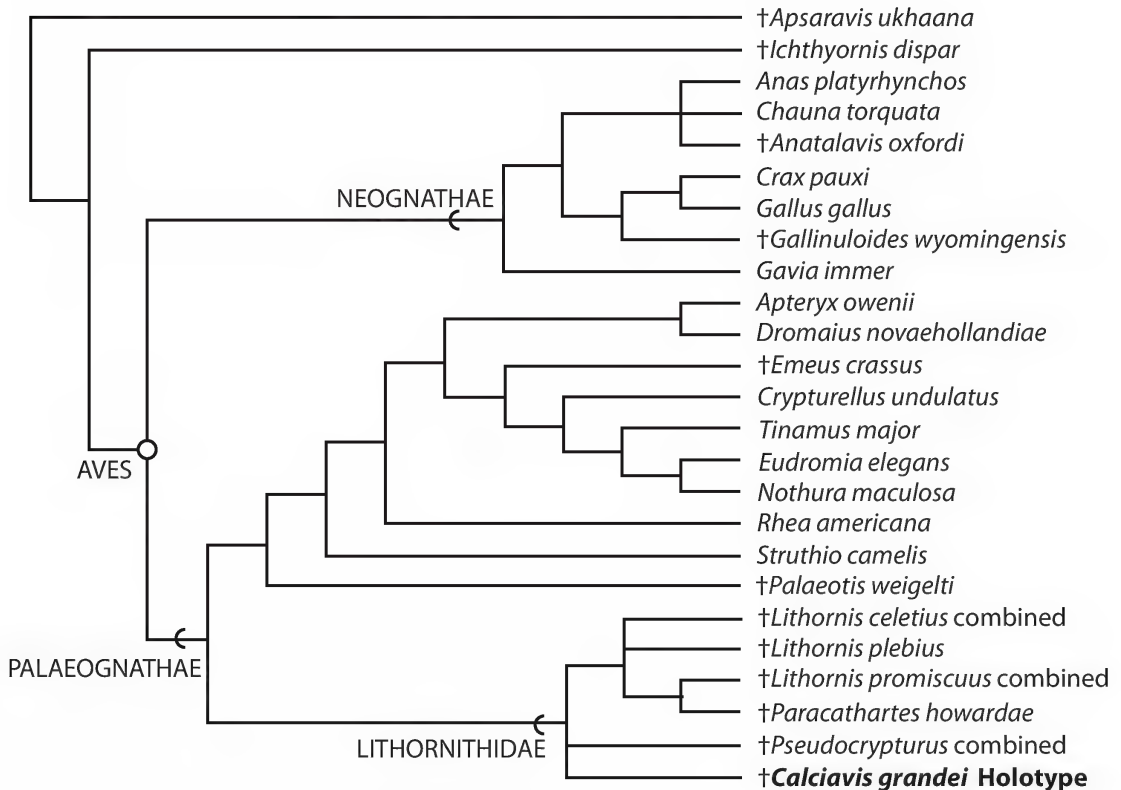


FIG. 29. Strict consensus when Palaeognathae relationships are constrained to the relationships found by Phillips et al. (2010).

SUPPORT: Aves – C66:1, C71:1, C93:1, C102:0, C113:1, C114:0, C115:0, C117:1, C118:2, C129:0, and C149:1; Palaeognathae – C5:1, C9:1, C31:1, C36:0, C42:0, C51:1, C62:1, C72:1, C137:1, C139:1, C167:1, and C180:0; Lithornithidae – C4:0, C12:0, C13:1, C16:1, C20:2, C60:1, C64:1, C67:2, C83:0, C103:0, C104:2, C112:0, C133:1, C141:1, C143:1, C150:1, and C177:1.

RESULTS: Lithornithidae again was found as the earliest diverging clade of the Palaeognathae, whereas Tinamidae is well nested within a paraphyletic Ratitae. The extinct *Palaeotis weigelti* was found as the sister taxon of all other Palaeognathae (exclusive of Lithornithidae). The resolution within Tinamidae and Anseriformes is lost, and taxa within Lithornithidae are only partially resolved with *Calciavis* and *Pseudocrypturus* placed as basal diverging members. The optimizations of the character states are nearly

identical to that found in the Phillips et al. (2010) constraint.

Palaeognath relationships of Mitchell et al. (2014) (fig. 31)

CONSTRAINT: The palaeognath relationships were constrained (as a backbone constraint in PAUP) to match the results of Mitchell et al. (2014). Note, the sampling of Mitchell et al. (2014) is greater than ours in this analysis; we do not include the elephant bird or cassowary. All other taxa were unconstrained.

SUPPORT: Aves – C66:1, C69:1, C71:1, C93:1, C102:0, C113:1, C114:0, C115:0, C117:1, C129:0, and C149:1; Palaeognathae – C5:1, C9:1, C31:1, C36:0, C42:0, C51:1, C72:1, C137:1, C139:1, C167:1, and C180:0; Lithornithidae – C4:0, C12:0, C13:1, C16:1, C60:1, C64:1, C67:2, C69:1,

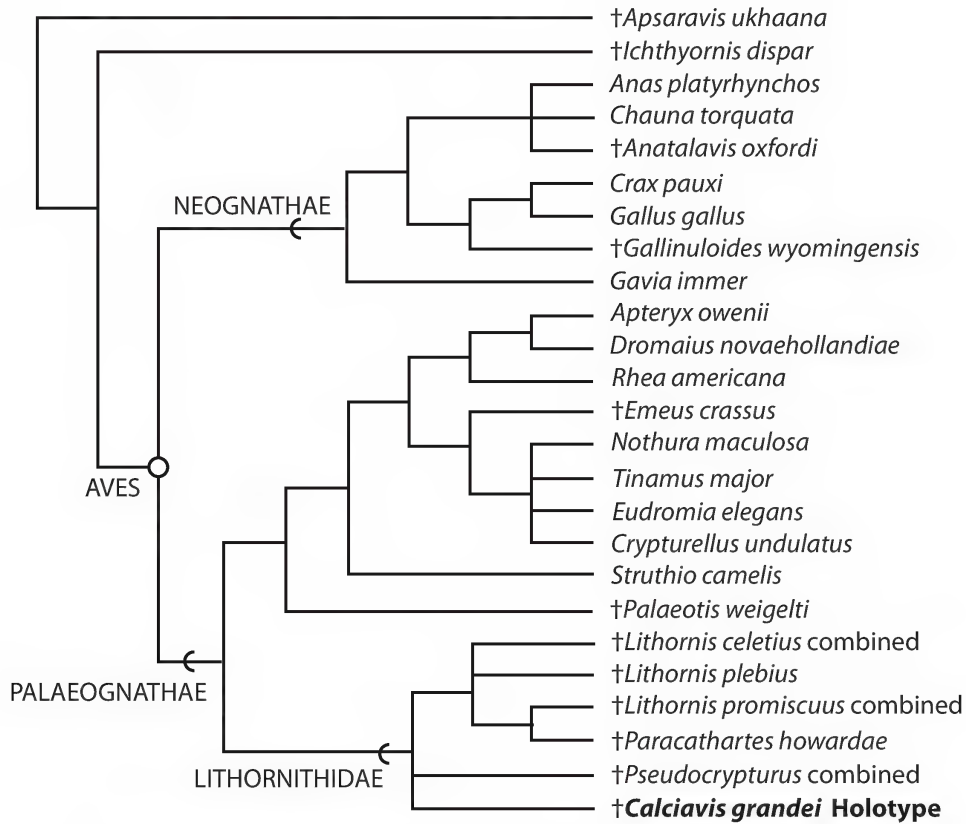


FIG. 30. Strict consensus when Palaeognathae relationships are constrained to the relationships found by Baker et al. (2014).

C83:0, C103:0, C104:2, C112:0, C133:1, C141:1, C143:1, C150:1, and C177:1.

RESULTS: As seen in the results from the analyses utilizing the Phillips et al. (2010) constraint and the Baker et al. (2014) constraint, Lithornithidae is not recovered with Tinamidae, but as basal within Palaeognathae as the sister taxon to all other included species. With this placement of the clade, the relationships among lithornithid species also are identical to those recovered the analyses using constraint trees based on the results of Phillips et al. (2010) and Baker et al. (2014).

ALTERNATIVE HYPOTHESES DISCUSSION: The relationships of nonpalaeognath Aves were generally similar to those recovered in the “core lithornithid” analysis. For example, neognath interrelationships remained nearly the same in

each constraint tree and ratite interrelationships also remain identical to those of the “core lithornithid” analysis unless ratites were specifically constrained (e.g., Phillips et al., 2010; Mitchell et al., 2014; Baker et al., 2014, constraints). However, the recovered relationships among lithornithids, and placement of Lithornithidae within Palaeognathae, varied significantly in each of the constraint runs depending on their closest outgroups. In all analyses, enforcing previous hypothesis of lithornithid relationships, *Lithornis* is paraphyletic with respect to a monophyletic Green River Formation lithornithid clade. In all analyses, enforcing constraints based on molecular sequence based phylogenetic hypotheses, Lithornithidae is not recovered with Tinamidae. Furthermore, a monophyletic *Lithornis* + *Paracathartes* clade is

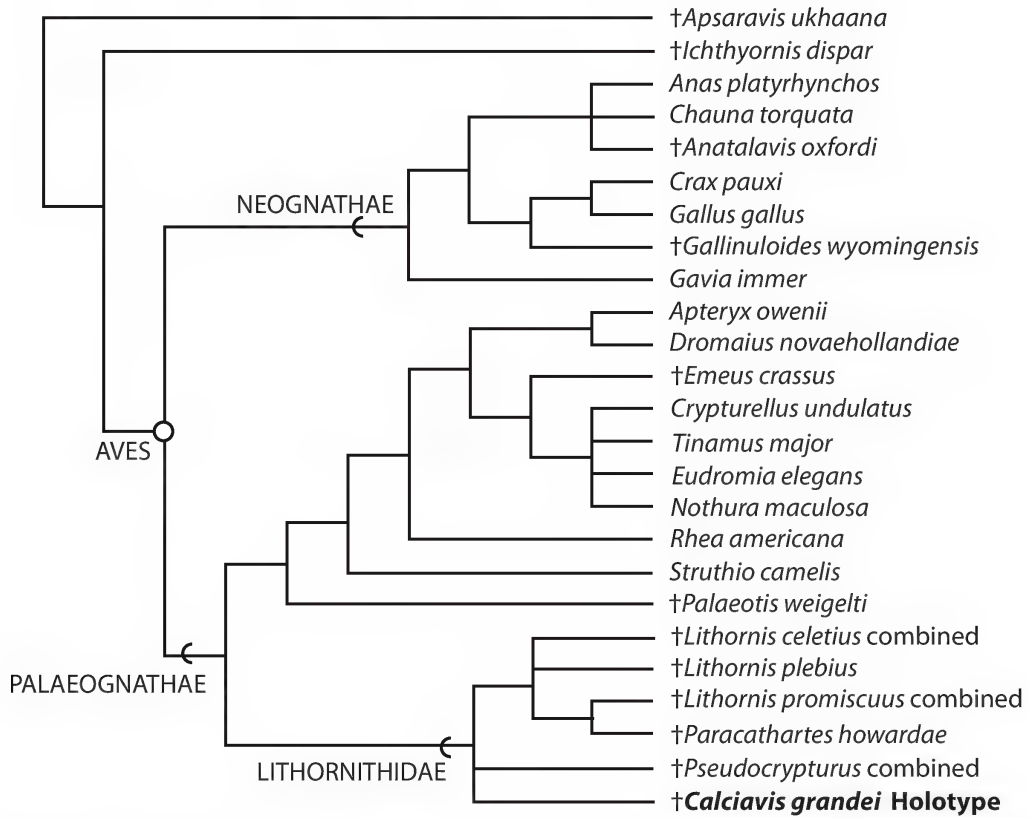


FIG. 31. Strict consensus when Palaeognathae relationships are constrained to the relationships found by Mitchell et al. (2014).

recovered, whereas the Green River Formation lithornithid relationships are unresolved in these analyses.

In all cases, the constraint trees had a higher number of steps and lower CI, RI, and RC values compared to the unconstrained analysis. In the analyses where Lithornithidae was found as monophyletic, the number of added steps was comparable. By contrast, the non-monophyly of Lithornithidae constraint added a significant number of steps (table 3). Constraining relationships to those obtained by Phillips et al. (2010), Baker et al. (2014), and Mitchell et al. (2014) led to an increase in the number of steps (41, 9% increase; 38, 8% increase; and 30, 6% increase, respectively) relative to the unconstrained tree. The number

of MPTs was highest in the unconstrained “total” analysis.

The support (i.e., apomorphies) for a monophyletic Lithornithidae in the constrained analyses was rather similar to the support found in the unconstrained trees. A few apomorphies were gained or lost relative to the unconstrained tree, but there was a core character set (C13:1, C38:1, C60:1, C67:1, C95:1, C143:1) that supported the clade. In the iteration where nonmonophyly of Lithornithidae was forced (i.e., *Paracathartes howardae* closer to ratites), none of the core lithornithid characters supported the monophyly without *Paracathartes howardae*. Instead, the core lithornithid apomorphies were spread across the branches of the Palaeognathae tree. Moreover, the only character state that supported

Paracathartes howardae closer to ratites than to other lithornithids was the reduction of the post-orbital process of the frontal (C17:1), a character state suggest by Houde (1988) in support of non-monophyly of Lithornithidae.

In the constraint analysis enforcing the relationships of Phillips et al. (2010), Lithornithidae was recovered as monophyletic and well supported (i.e., 18 unambiguous apomorphies). The support of this clade contained most, but not all of the core lithornithid apomorphies (4 total) of the unconstrained analysis. The additional apomorphies supporting the clade previously supported a Lithornithidae + Tinamidae clade in the unconstrained tree. Thus, part of the addition of the number of steps in the Phillips et al. (2010) constraint tree was the result of the independent origin of apomorphies of Lithornithidae and Tinamidae in the unconstrained analyses.

The character support for Aves and Palaeognathae varies throughout the alternative hypotheses iterations, but character support was rather constant when the relationships of the earliest member of the clade were not constrained. The biggest differences in character support for Aves and Palaeognathae relative to the unconstrained analysis occurred when Lithornithidae was constrained to a position outside Aves. Many of the character states that supported Aves in the unconstrained analysis supported a Lithornithidae + Aves clade in the constraint tree, and apomorphies that once supported Lithornithidae + Tinamidae, Lithornithidae + Tinamidae + ratites, and Palaeognathae in the unconstrained analysis were spread across the tree. Interestingly, two apomorphies that support Aves in both the unconstrained and "Lithornithidae outside Aves" are related to the increase of number of vertebrae in the synsacral series (C69:2 and C70:2) relative to the plesiomorphic condition in Avialae. Lithornithids, tinamous, and outgroups of Aves (e.g., *Ichthyornis*; Clarke, 2004) have 12 synsacral vertebrae whereas galloanserines and other palaeognaths generally have 15 or more.

DISCUSSION

SPECIES DIVERSITY OF GREEN RIVER FORMATION LITHORNITHIDS

The Fossil Butte Member of the Green River Formations has produced the largest sample of lithornithids skeletons to date. Here, we add five new specimens for a total of seven partial skeletons of lithornithids from near contemporaneous localities spanning both F1 and F2 deposits of Fossil Lake (of Grande and Buchheim, 1994). The morphological differences among the Green River Formation specimens are few, but this is not surprising given that Houde (1988) found little morphological variation across the skeleton of North American lithornithids spanning 10–15 million years. Here, we argue that there is a minimum of two species-level lithornithid taxa from the Green River Formation. We discuss the possible ontogenetic status of the specimens, as well as morphological and proportional differences to consider the possibility that one species-level taxon can explain all these data.

ONTOGENETIC AGE: The ontogenetic stages represented by the Green River Formation lithornithids is important for considering their taxonomy. Histological analysis of long bones of avians can directly determine what part of the growth cycle an avian had reached at death (Chinsamy et al., 1995; Chinsamy and Elzanowski, 2001). Because, unfortunately, this method is destructive, it was not used here. Instead, we turned to a non-destructive method that correlates the surface texture of long bones to skeletal maturity in avians (e.g., "textural aging" of Tumarkin-Deratzian et al., 2006; 2007; Watanabe and Matsuoka, 2013). This method of evaluating skeletal maturity is determined by examining the surface texture of a long bone and its correlation with the histology of the same bone. For example, a fibrous external surface of a long bone correlates with the early faster growth (woven bone) of a skeletally immature avian whereas a smooth external surface of a long bone correlates with the later, zonal lamellar

growth strategy of skeletally mature avians (Tumarkin-Deratzian et al., 2007). Furthermore, this method of accessing skeletal maturity appears to be valid in fast growing archosaurs (e.g., pterodactyloid pterosaurs, Bennett, 1993; possibly large theropods, Carr, 1999; early avialans, Erickson et al., 2009), but not in slower growing archosaurs (e.g., *Alligator mississippiensis*, Tumarkin-Deratzian et al., 2007).

Using this nondestructive method, we evaluated the skeletal maturity of Green River Formation lithornithids. The surface textures of long bones of both the holotype (AMNH 30578) and referred specimen (AMNH 30560) are nearly smooth. Given that these specimens were buried relatively quickly after death with finely preserved features and were prepared extremely carefully to preserve these features, it is clear that the smooth external surfaces were not taphonomic artifacts nor mechanically produced. Thus, it is clear that the *Calciavis grandei* specimens were skeletally mature at death. The ontogenetic age of the holotype of *Pseudocrypturus cercanaxius* (USNM 336102) cannot be determined using these methods confidently because no long bone elements are preserved. However, the same-sized referred specimen (Siber and Siber specimen, USNM 424078 [cast]) does preserve long bone elements. We assessed the skeletal maturity of *Pseudocrypturus cercanaxius* from a highly detailed plaster cast. The external textures of the long bones are as smooth as those of *Calciavis grandei* and thus, the referred specimen and likely the holotype were also skeletally mature. Note, however, it is possible that the mold was not detailed enough to pick up fine striations on the outside of long bones. Nevertheless, both the holotype and referred specimens of *Pseudocrypturus cercanaxius* have larger skulls than that of the skeletally mature *Calciavis grandei* and, therefore, *Pseudocrypturus cercanaxius* must have reached an absolute larger head size. The long bones of the other Green River Formation lithornithids (FMNH PA 739, FMNH PA 729, and WGS 41-2001) all have smooth external surfaces, and thus also appear to be skeletally mature.

As a part of this skeletally maturity evaluation, we also examined the maturity of *Lithornis celetius* (USNM 290554) and *Paracathartes howardae* (USNM 361407) because these specimens have both histological sections and long bones that can be evaluated for external texture. The carpometacarpus of *Lithornis celetius* (USNM 290554) has a smooth texture across the element. Similarly, the long bones of *Paracathartes howardae* (e.g., femur, USNM 361412) found with USNM 361407 also has a smooth texture across the element. Therefore, the external features of these specimens indicate they are from a skeletally mature individual. Furthermore, this age assessment is supported by histological sections of the tibiotarsi of both taxa (Houde, 1988). The histological sections show a distinct transition from woven bone to more parallel-fibered bone in the outer cortex of the section. Both individuals had nearly stopped growing at prior to death. The similar texture of the long bones of individuals of *Lithornis celetius*, *Paracathartes howardae*, *Calciavis grandei*, and *Pseudocrypturus cercanaxius* suggests that all these individuals were skeletally mature at death. Thus, Houde's (1988) original differentiation of species-level taxa of lithornithids based on size appears valid, and these species-level boundaries are backed up by morphology (see below).

MORPHOLOGICAL DIFFERENCES: The first taxon recognized from the Green River Formation was *Pseudocrypturus cercanaxius* (Houde, 1988). Unfortunately, the well-preserved and prepared holotype (USNM 336102) consists of only a laterally compressed skull and partially preserved cervical series, thus making comparison to other lithornithids and referring incomplete lithornithids specimens from the Green River Formation difficult (fig. 32). Of the original diagnosis provided by Houde (1988), only the listed cranial characters (e.g., robust lateral nasal bar, small pterygoid fossa, palatine with posteriorly (= caudally) directed process, vomer that articulates with the premaxilla) can be used for comparison and for referring specimens to *Pseudocrypturus cercanaxius*. This combination of

character states of the skull is unique (see Houde, 1988, and diagnoses below). The noncranial character states in the diagnosis of *Pseudocrypturus cercanaxius* comes from the referred specimen (Siber and Siber specimen, USNM 424078 [cast]) including: sternum with shallow notches in the posterior margin; coracoid with long slender shaft; scapula with straighter shaft and more pronounced acromion; tarsometatarsus with symmetrical trochlea III and winglike processes of trochleae II and IV; and short limbs. Most of the character states of the holotype skull of *Pseudocrypturus cercanaxius* cannot be evaluated in the referred specimen. The absolute length and proportions of the skull (table 4) and its individual elements are identical in the holotype and the referred specimen; therefore, we concur with Houde (1988) and refer the Siber and Siber specimen to *Pseudocrypturus cercanaxius*. Consequently, nearly the entire anatomy of *Pseudocrypturus cercanaxius* is visible and serves as a comparison to the other Green River Formation lithornithids from nearby localities.

The holotype of *Calciavis grandei* has elements directly comparable to both the holotype and referred specimen of *Pseudocrypturus cercanaxius*. The morphological features of *Calciavis grandei* and *Pseudocrypturus cercanaxius* are nearly identical, and both taxa are about the same in body size. In our phylogeny, the character scores are identical (when scorable) between the holotype of *Calciavis grandei* and the holotype of *Pseudocrypturus cercanaxius*, and the holotype of *Calciavis grandei* and the referred specimen of *Pseudocrypturus cercanaxius* are scored for the same character states except for character 18. In *Pseudocrypturus cercanaxius*, the skull is longer than the humerus, whereas in *Calciavis grandei* the humerus is clearly longer than the cranium. Furthermore, the skull is longer than the tibiotarsus in *Pseudocrypturus cercanaxius*, whereas the tibiotarsus is distinctly longer than the skull in *Calciavis grandei*.

The skeletal proportions of *Pseudocrypturus cercanaxius* and *Calciavis grandei* are different further supporting their identity as distinct species

(table 1). For example, the length of the femur of the holotype of *Calciavis grandei* is longer than that of the referred specimen of *Pseudocrypturus cercanaxius*, but the length of the sternum of *Pseudocrypturus cercanaxius* is absolutely longer than that of the holotype of *Calciavis grandei*. By contrast, similar proportions (i.e., humerus longer than the cranium; in limb elements), as well as morphological features, led to our referral of AMNH 30560 to *Calciavis grandei*. However, AMNH 30560 is not exactly the same size as the holotype (~90% the size of the holotype), and the precise scaling proportions of some limb elements are not the same (e.g., the skull of the referred specimen is ~93% that of the holotype whereas the tibiotarsus length is 87% that of the holotype). It is not clear whether these minor proportional differences represent actual differences (e.g., individual variation of sexual dimorphism) or could be explained by taphonomic processes during fossilization such as compaction.

In sum, the differences in skull size relative to long bones in the skeletons easily differentiates *Pseudocrypturus cercanaxius* from *Calciavis grandei* given that the holotype and referred specimens represent skeletally mature adults. Differentiation of contemporaneous species-level taxa from proportional differences in the skeleton is practiced in avian studies of both extant and extinct (e.g., Olson and Matsuoka, 2005) taxa. As support, we examined 19 specimens from one population of the tinamou *Eudromia elegans* (tables 5, 6), a close relative of lithornithids. We measured individual elements and skull length to compare to *Pseudocrypturus cercanaxius* and *Calciavis grandei*. In this small sample *Eudromia elegans*, it was clear there was overall variation in size of each element. However, the range of lengths and the standard deviation of each element was within 5% the length of each element. Ergo, *Eudromia elegans* proportions differ little and show a much smaller range of variation of that of the *Pseudocrypturus cercanaxius* and *Calciavis grandei* specimens taken together.

There appear to be only two presently diagnosable species from the Fossil Butte Member of

TABLE 4
Ratios between different elements of the Green River Formation lithornithids
 X = measurements that could not be made.

Specimen	Skull/ humerus	Skull/ femur	Humerus/ femur	Carpo/ meta
<i>Calciavis</i> AMNH 30587	0.94	1.22	1.29	0.77
<i>Calciavis</i> AMNH 30560	0.98	X	X	0.71
<i>Pseudocrypturus</i> Siber	1.14	1.53	1.34	0.87
<i>Pseudocrypturus</i> FMNH PA 739	X	X	X	0.86
Average	1.02	1.37	1.32	0.80
Standard deviation	0.11	0.22	0.03	0.08

the Green River Formation, *Pseudocrypturus cercanaxius* and *Calciavis grandei*. Yet there are a number of other specimens from the same unit that are far from complete and lack preservation of differentiating morphologies (see above) between the two recognized species-level taxa. FMNH PA 739 and WGS 41-2001 appear to share a more similar absolute size and similar proportions of elements with *Pseudocrypturus cercanaxius* than with *Calciavis grandei*. Likewise, FMNH PA 729 appears to share a similar absolute size and similar proportions of elements with *Calciavis grandei* than *Pseudocrypturus cercanaxius*. Nevertheless, all three specimens (FMNH PA 739, FMNH PA 729, WGS 41-2001) lack both a humerus and a skull and, as a result, they are not obviously referable to *Calciavis grandei* or *Pseudocrypturus cercanaxius* based on presently available morphological evidence. Furthermore, these three specimens are incomplete, and we cannot reject the notion that they represent different species-level taxa. Therefore, we assign FMNH PA 739, FMNH PA 729, and WGS 41-2001 only to Lithornithidae spp., following the results of our phylogenetic analyses.

Even though the Green River Formation lithornithids are scored nearly identically in our phylogenetic analysis, they do appear to share a few character states that differ from those of other lithornithids. For example, all the Green River Formation lithornithids have a scapular blade that terminates in a relatively broad tip

(C106:0) rather than a finely tapered point. Additionally, tarsometatarsal trochlea II and IV are approximately equal in distal extent (C180:0), but other lithornithids have a metatarsal II that is shorter than trochlea IV (C180:1). Furthermore, the medial portion of the pterygoid anterior to the facet for the articulation of the basiptyergoid process is straight (C22:0) in the Green River Formation lithornithids, but medially expanded in all other lithornithids.

SEXUAL DIMORPHISM: Extant birds can show differences in plumage patterning, behavior, and size between the sexes (e.g., Owens and Hartley, 1998; Dunning, 2008). In the fossil record, detection of sexual dimorphism is almost entirely restricted to differences in absolute size at skeletal maturity because of the rarity of preservation of a large sample of plumage or evidence of behavior in fossils. The differences between the two Green River Formation species, *Calciavis grandei* and *Pseudocrypturus cercanaxius*, are only in the length of the skull relative to the lengths of long bones (e.g., humerus and tibiotarsus), and in proportional differences in the scaling of long bones (e.g., tibiotarsus versus tarsometatarsus) relative to size. We were not able to find any extant cases among avian of such a large difference of relative skull size between the sexes. For example, in the skeletally mature population of the tinamou *Eudromia elegans* we considered, the proportions of the skull versus long bones (e.g., tibiotarsus) did not differ more than

TABLE 5
Selected measurements of an adult sample ($n = 19$) of the tinamous *Eudromia elegans*
 Measurements rounded to nearest 1/10 mm. X = measurements that could not be made. All specimens are
 curated at USNM

Specimen (USNM)	Skull length	Mandible length	Sternum length	Humerus length	Ulna length	Carpo- meta- carpus length	Femur length	Tibiotar- sus length	Tarso- metatar- sus length
345096	62.5	51.2	X	62.7	67.4	36.8	58.8	84.2	51
345093	61	49.5	85.7	60.1	63.3	35	54.6	77	46.6
345097	64.9	54.6	96.6	62.9	67.2	36.4	57	83	48.9
345015	63.8	53	94.4	61.3	66.3	36.4	58.5	83.5	50.1
344966	62.1	52.3	94.1	64.2	64.1	35.9	61	83.6	48.5
345014	65.1	54.8	86.3	60.5	63.1	35.5	56.1	82.1	48.5
347009	63.4	52.5	89.3	61.5	64.4	35.3	58.6	82.9	47.6
345016	60.9	49.1	87.7	58.9	63	35.2	56.8	78.6	47.7
345052	62.5	52	98.9	62.1	65.9	36.8	58.5	81.1	47.3
345095	63.7	46.1	94.1	60.2	63.2	35.9	56.3	78.5	47.8
344991	62.7	50.2	83.9	60.3	64.4	36.3	X	82.3	50.3
345094	62.2	53.2	95.4	63.5	68.1	37	58.4	84.3	47.9
346848	61.5	50.9	91.5	60.6	63.2	35.1	57.5	79.6	47.4
345019	58.7	48	84.6	59.3	63.8	34.6	57.1	80.7	46.8
345064	61.7	46.3	92.5	69.2	62.9	35	56.5	83.5	49.2
345018	61.3	49.8	82	58.9	63.1	35.5	56.9	79	46.8
345472	59.2	49.4	86.5	56.6	60	33.5	55.3	80.2	47.1
345063	X	X	X	56.8	59.4	33.3	54.2	X	45
227489	X	51.5	94.9	65.4	68.7	36.2	60.1	81.8	48.8
Average	62.2	50.8	90.5	61.3	64.3	35.6	57.3	81.4	48.17
Standard deviation	1.74	2.5	5.09	2.98	2.48	1.03	1.78	2.21	1.45

a few percent compared to the total length (table 6). Unfortunately, the sex and weight of each specimen of *Eudromia elegans* was not recorded; thus, it is possible that sample contained male-only or female-only members.

A close relative of lithornithids, the recently extinct moas from New Zealand, had a unique system of sexual dimorphism only recently recognized (Bunce et al., 2003). Previously, three size classes of *Dinornis* were divided into three species (*D. giganteus*, *D. novaezealandiae*, and *D. struthoides*) with differences in cranial morphology as supporting evidence of species-level dif-

ferences (Worthy, 1994). The recovery of mitochondrial data from each of the three size classes showed that: (1) all size classes belonged to the same species-level taxon; and (2) through sex determination using the same molecular data, the larger-size classes (*D. giganteus* and *D. novaezealandiae*) belonged to females and the smallest size class (*D. struthoides*) represented males (Bunce et al., 2003). Thus, *Dinornis* demonstrated sexual dimorphism in absolute body size. Yet, we were interested in the proportional differences between the skull and long bones (e.g., tibiotarsus and femur) among the size

TABLE 6
 Ratios between different elements of *Eudromia elegans*
 X = measurements that could not be made.

Specimen (USNM)	Skull/ humerus	Skull/ femur	Humerus/ femur	Carpo/ meta
345096	1	1.06	1.07	0.72
345093	1.01	1.12	1.11	0.75
345097	1.03	1.14	1.1	0.74
345015	1.04	1.09	1.05	0.73
344966	0.97	1.02	1.05	0.74
345014	1.08	1.16	1.08	0.73
347009	1.03	1.08	1.05	0.74
345016	1.03	1.07	1.04	0.74
345052	1.01	1.07	1.06	0.78
345095	1.06	1.13	1.07	0.75
344991	1.04	X	X	0.72
345094	0.98	1.07	1.09	0.77
346848	1.01	1.07	1.05	0.74
345019	0.99	1.03	1.04	0.74
345064	0.89	1.09	1.22	0.71
345018	1.04	1.08	1.04	0.76
345472	1.05	1.07	1.02	0.71
345063	X	X	1.05	0.74
227489	X	X	1.09	0.74
Average	1.01	1.08	1.07	0.74
Standard deviation	0.04	0.04	0.05	0.02

classes in *Dinornis*. Using data from skulls, tibiotarsi, and femora from all three size classes presented by Worthy (1994), we show that the differences in proportions across the three size classes were relatively similar (table 7), and far from the differences between the Green River Formation lithornithids *Calciavis grandei* and *Pseudocrypturus cercanaxius* (table 4). Therefore, the proportional differences among proposed lithornithids species-level taxa are different from the extreme sexual dimorphism proposed for the moa, *Dinornis*.

Both *Calciavis grandei* and *Pseudocrypturus cercanaxius* are from contemporaneous deposits

(Grande and Buchheim, 1994), although both species have not been found at the exact same locality within the F-2 deposits of Fossil Lake. Houde (1988) noted that *Lithornis promiscuus* and *Lithornis plebius* are always found together at the same localities in the Willwood Formation (Clarkforkian) of Wyoming. Houde (1988) further entertained the hypothesis that these two taxa represent sexual dimorphs of one species-level taxon, but provided a number of morphological and size differences and hypothesized that the differences were diagnostic to specific taxa. If the differences in size (*Lithornis plebius* is about 75% the size of *Lithornis promiscuus*) represent

TABLE 7
Dinornis comparison
Data from Worthy (1994).

	Cranium average length	Tibiotarsus average length	Femur average length	Cranium/ tibiotarsus	Cranium/ femur	Tibiotarsus/ femur
Large form = “ <i>D. giganteus</i> ”	215.6	820.1	381.6	0.26	0.56	2.14
Medium form = “ <i>D. novaezealandiae</i> ”	183.4	648.6	319.6	0.28	0.57	2.02
Small form = “ <i>D. struthoides</i> ”	164.9	542.2	284.4	0.30	0.57	1.90

dimorphic differences in a single species-level taxon, this dimorphism would not accord with that of *Calciavis grandei* and *Pseudocrypturus cercanaxius*, given that both proposed species-level taxa are about the same size but have slight proportional differences.

The lack of major morphological differences between skeletal elements across the body among males and females of a single population in extant and extinct avians provides support that the major differences in the skull length versus long bone length in *Calciavis grandei* and *Pseudocrypturus cercanaxius* represents taxonomic variation and not sexual dimorphism. Nevertheless, it remains possible that the proportional variation in the length of the skull versus other long bone elements could be a property of single species-level taxon of lithornithid or lithornithids as a whole. At this time, however, we hypothesize that the differences *Calciavis grandei* and *Pseudocrypturus cercanaxius* represent taxonomic differences.

MONOPHYLY OF LITHORNITHIDAE AND
DIAGNOSTIC FEATURES OF THE CLADE

Lithornithidae was previously considered a monophyletic assemblage or a basal stock of palaeognaths that gave rise to other palaeognath lineages (Houde, 1988). For the first time, we tested the monophyly of Lithornithidae based on scoring specimens and species-level taxa individually in a phylogeny, sampling the avian stem and extinct and extant members of Palaeognathae and basal Neognathae. We find support

for this clade within Palaeognathae. Unfortunately, we failed to find any resolution within Lithornithidae with our data set. Thus, we were unable to test the monophyly of *Lithornis* in this analysis. Nevertheless, Lithornithidae is a diagnosable clade that is restricted to the Paleogene (late Paleocene to the late Eocene) of North America and Europe (see below).

Character support for Lithornithidae as a monophyletic clade is relatively high in both the “total” and “core lithornithid” analyses. However, some of the apomorphies supporting Lithornithidae in this analysis represent plesiomorphies in other phylogenetic analyses sampling other avian taxa (e.g., Mayr and Clarke, 2003). For example, in this analysis, the presence of an osseous bridge from transverse process to the postzygapophysis of the third cervical vertebra (C64:1) optimized as an apomorphy of Lithornithidae. This character state, however, occurs in a number of avians (e.g., basal neognath clades) at the base of the tree that were not sampled in this analysis (see Mayr and Clarke, 2003). Similarly, the presence of 12 synsacral vertebrae (C69:0) in lithornithids optimizes as an apomorphy of the clade. Among the palaeognaths sampled here and the structure of the interrelationships of those taxa, the presence of 12 synsacral vertebrae is apomorphic. However, the presence of 12 synsacral vertebrae is plesiomorphic for Aves (see Clarke, 2004), and thus, this character state in lithornithids likely represents a plesiomorphic character state in Aves.

Although, there are a number of character states supporting Lithornithidae that previously

were found to represent plesiomorphies of either Palaeognathae or Aves in other analyses. Lithornithidae is supported as a monophyletic clade by a combination of apomorphies with high CIs in our analyses, and other character states that occur in other avian clades, but appear either to be independently evolved in lithornithids or to represent a unique combination of character states not present in any other avian group. In the following character list of lithornithid apomorphies, we focused on character states that: (1) were apomorphic in both the “total” and “core lithornithid” analyses; (2) were frequently apomorphic in the constraint trees (see Constraint Trees and Alternate Hypotheses of the Relationships of Lithornithidae) and (3) are not obviously plesiomorphic for Aves. The following list is also similar to the apomorphy list provided by Houde (1988) in his comprehensive study of lithornithids.

Lithornithid apomorphies:

- (1) broad, flat ventral process of the lacrimal in lateral view (C13:1) (figs. 32–34);
- (2) quadrate with a small fossae on the posterior side of the body (C38:1) (fig. 34);
- (3) short fingerlike retroarticular process just posterior to the articular facet of the mandible (C60:1) (figs. 34, 35);
- (4) centrally located ovoid foramina on the lateral surfaces of the centra of the thoracic vertebrae (C67:2) (figs. 7, 34);
- (5) foramina present on the posteroventral surface of the hooked acrocoracoid process of the coracoid (C95:1) (fig. 34);
- (6) acromion of the scapula laterally hooked tip with small foramina on the posterior side (C104:2) (fig. 34) (possible autapomorphy);
- (7) infratrochlearis fossa deeply excavating the proximal surface of the pisiform process on the ventral surface of the carpometacarpus (C136:1) (fig. 34);
- (8) distinct tuber present on the ventral side of the proximal portion of metacarpal III (C143:1) (fig. 34).

Lithornithidae is diagnosed by the combination of apomorphies presented above in which

few of the apomorphies represent nonlocal autapomorphies of the clade. With that said, we urge future workers to assign taxa to Lithornithidae only if they have a majority of all of the apomorphies in a partial or complete skeleton. Assignment of an isolated avian element to Lithornithidae based on a single apomorphy on the presented list will be poorly supported given the high rates of homoplasy present in avians (see Mayr and Clarke, 2003; Livezey and Zusi, 2007). Consequently, the assignment of isolated bones to Lithornithidae is not recommended. For example, the oldest possible members of Lithornithidae are represented by an isolated scapula from the Late Cretaceous/early Paleocene of New Jersey (Parris and Hope, 2002) and a partial coracoid named *Fissuravis weigelti* Mayr, 2007, from the Paleocene of Walbeck in Germany (Mayr, 2007). Both isolated bones may be the remains of Lithornithidae, but morphologies approaching the hooked acromion of the Lithornithidae are approached in several stem ornithurine birds in the Mesozoic Era (Clarke, 2004) and the isolated coracoid fragment does not appear to bear any lithornithid character state other than a similar size. In fact, the coracoid appears to be lacking small foramina present posteroventral surface to the hooked acrocoracoid process of the coracoid (C95:1), one of the character states listed above in the diagnosis. As such, isolated bones are nearly impossible to assign to Lithornithidae based on our phylogenetic hypothesis and further analysis.

IS *PARACATHARTES HOWARDAE* PART OF
LITHORNITHIDAE?

Houde (1988) hypothesized that *Paracathartes howardae* was not a lithornithid, but may be closer to ratites than to other lithornithids. He cited two pieces of evidence: (1) a reduced and rounded postorbital process of the frontal; and (2) a similar histologic growth pattern of *Paracathartes howardae* and ratites. In our analysis, we find *Paracathartes howardae* usually well nested (in the MPTs) within Lithornithidae, and therefore, the reduced and broad postorbital process

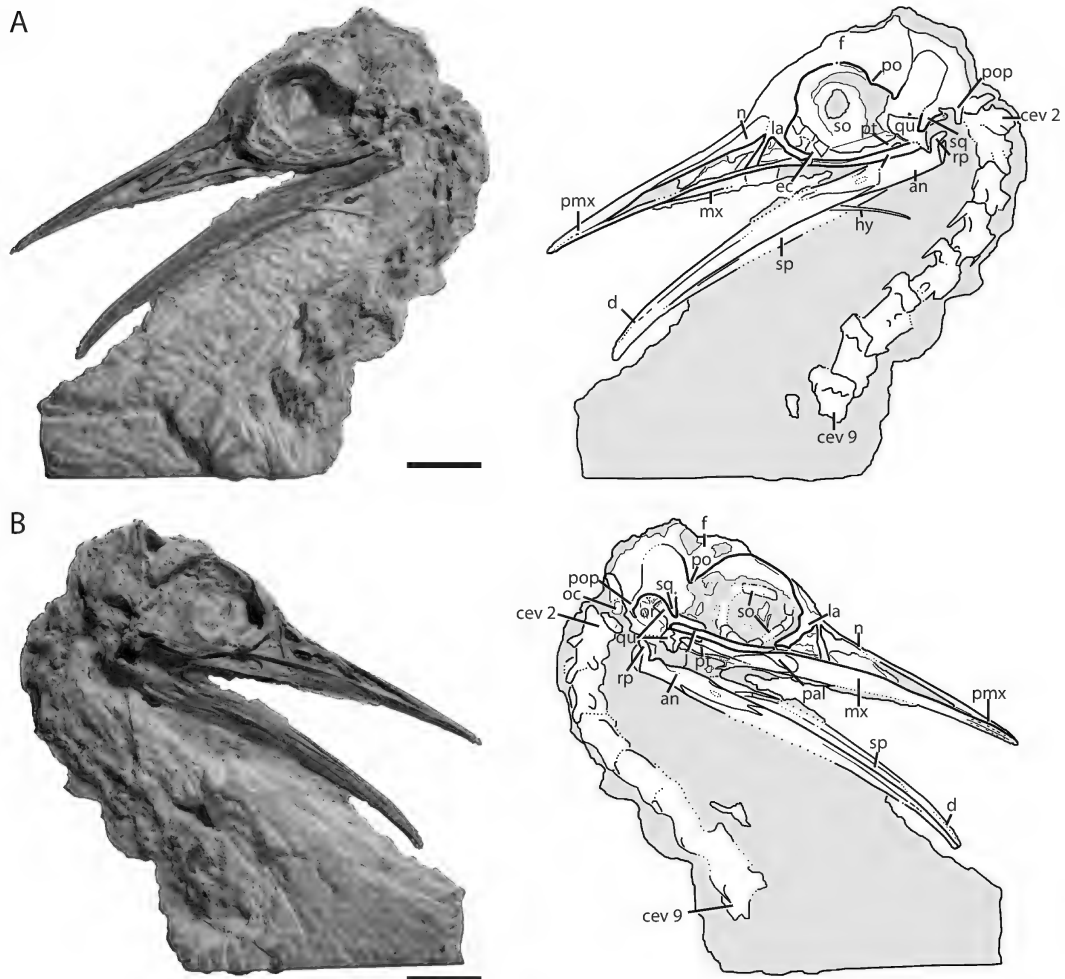


FIG. 32. The holotype skull and cervical vertebrae of *Pseudocrypturus cercanaxius* (USNM 336103) in **A**, left lateral and **B**, right lateral views. Scale = 1 cm. See anatomical abbreviations.

shared by *Paracathartes howardae* and ratites (char. 17 here) likely is convergent. The growth pattern shared between *Paracathartes howardae* and ratites appears to be more similar to each other than to *Lithornis* (Houde, 1988; fig. 28) because *Paracathartes howardae* and ratites share a general growth pattern of concentric rings of vascularization throughout the cortex. However, the vascular canal pattern present in *Paracathartes howardae* is intermediate in morphology between ratites and *Lithornis* (Houde, 1988). The dominate orientation of the vascular canals in

histological section of *Paracathartes howardae* is longitudinal like that of *Lithornis*, but the longitudinal vascular canals are arranged circumferentially (or plexiform; see Erickson et al., 2009) throughout the cortex like that of ratites. Yet, ratites appear to nearly completely lack longitudinally oriented canals. Additionally, recent work on body size and growth strategy in stem birds (Padian et al., 2004; Erickson et al., 2009; Werning et al., 2011), particularly vascularization patterns, has shown that body size and vascularization are correlated; smaller animals (e.g., the

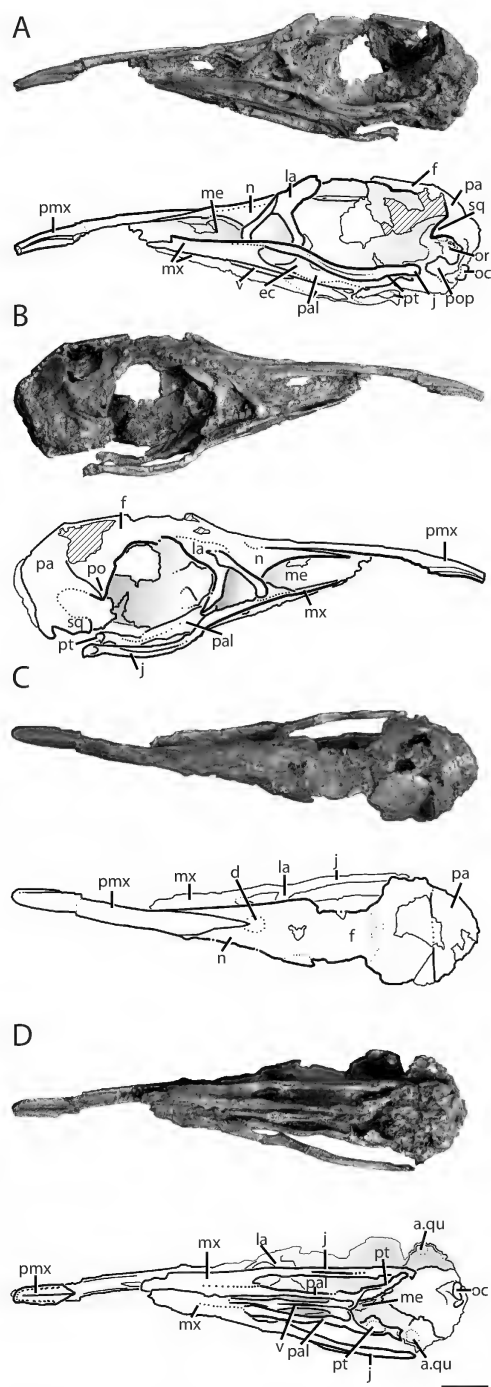


FIG. 33. Nearly complete skull (USNM 391983) referred to *Lithornis promiscuus* in **A**, left lateral, **B**, right lateral, **C**, dorsal, and **D**, ventral views. Scale = 1 cm. See anatomical abbreviations.

early avialan *Archaeopteryx lithographica*) have dominantly longitudinally oriented vascularization whereas larger animals (e.g., the oviraptorid theropod *Citipati osmolskae*) are dominated by circumferentially oriented (or plexiform) vascularization. *Paracathartes howardae* was estimated to be nearly twice as large as other lithornithids (Houde, 1988) and, therefore, body size may explain the similarity in circumferentially oriented vasculature in *Paracathartes howardae* and ratites, not homology or phylogeny.

We further tested Houde's (1988) hypothesis of the phylogenetic position of *Paracathartes howardae* in a constraint tree and found that if *Paracathartes howardae* is more closely related to ratites than to other lithornithids, one would need to add 17 more steps to our original unconstrained "core lithornithid" analysis. Moreover, there was almost no character support for this hypothesized relationship. Therefore, our data support *Paracathartes howardae* as a lithornithid.

WHAT IS THE BASALMOST LITHORNITHID LINEAGE?

We were unable to obtain any resolution of relationships within Lithornithidae in the most inclusive and unconstrained analysis (fig. 24). *Calciavis grandei* and *Pseudocrypturus cercanaxius* are found as sister taxa of all other lithornithids in a majority of the MPTs in the "core lithornithid" analysis. In the constrained analyses, when account relationships supported by molecular data (figs. 29–31) are taken into account, the position of the Green River Formation taxa relative to a monophyletic *Paracathartes* + *Lithornis* clade is again unresolved. By contrast, in the constrained analyses, when the position of a lithornithid clade is shifted, *Lithornis* is recovered as paraphyletic and the Green River Formation taxa are a well-nested subclade. None of these subclade relationships is robustly supported. However, *Calciavis grandei*, *Pseudocrypturus cercanaxius*, and all other Green River Formation lithornithid specimens not assignable to either taxon share character states

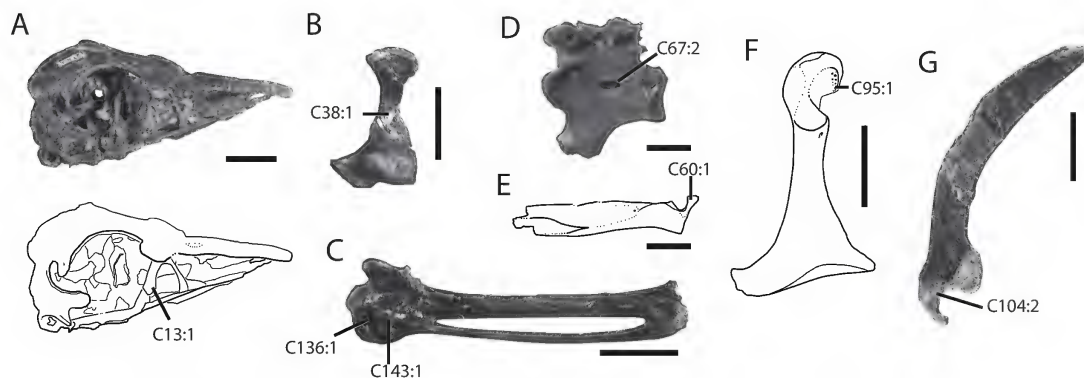


FIG. 34. **A**, Photograph and interpretative line drawing of the holotype skull of *Lithornis celetius* (USNM 290601) in right lateral view. **B**, Right quadrate of *Lithornis promiscuus* (USNM 336535) in posterior view. **C**, Left carpometacarpus of *Lithornis promiscuus* (USNM 336535) in ventral view. **D**, Isolated thoracic vertebra of *Lithornis* (NHMUK A5425) in left lateral view. **E**, Line drawing of the right half of the mandible of the holotype of *Lithornis promiscuus* (USNM 336535) in lateral view. **F**, Line drawing of the left coracoid of *Paracathartes howardae* (USNM 361417) in dorsal view. **G**, Left scapula of *Paracathartes howardae* (USNM 361419) in dorsal view.

that are not present in other lithornithids (e.g., C22:0, C106:0, C180:0). *Pseudocrypturus cercanaxius* exclusively shares small posteriorly directed processes of the palatine (C25:2) with Tinamidae, the sister taxon of Lithornithidae in our analysis. Inclusion of these taxa as separate terminals in future more-inclusive analyses may help resolve the placement of Lithornithidae and would reveal whether these character states are plesiomorphies or apomorphies for the clade.

In the analyses recovering a paraphyletic *Lithornis* (figs. 25, 27), *Lithornis celetius* is placed as the sister taxon of all other lithornithid species. The skull of *Lithornis celetius* is the only lithornithid to bear the plesiomorphic condition of a rounded posterolateral portion of the nasal (C7:0). *Lithornis celetius* also has a well-developed preacetabular pectineal process of the pubis (C154:2), a character state present in Tinamidae and other palaeognaths, but not in any other lithornithid. *Lithornis celetius* also bears a posteriorly elongated and tapering ischium (C156:1), a plesiomorphic character state found outside Aves, but not among any other lithornithid. To date, *L. celetius* is the oldest-named taxon (see appendix 2), but from our analysis, it is not clear whether the charac-

ter states shared with Tinamidae are plesiomorphic or independently derived.

VARIATION WITHIN LITHORNITHIDAE

In an attempt to resolve the interrelationships of Lithornithidae, we added a number of characters that were variable among observed lithornithids. Some of these characters, although variable in lithornithids, were also variable across avian taxa included in the analysis, could not be scored in a number of lithornithid taxa, or represented autapomorphies (see appendix 2). Nevertheless, the added characters did not help resolve the interrelationships of Lithornithidae but may be useful for future more-inclusive analyses. With a few exceptions, lithornithid holotypes are mostly complete and well preserved relative to other extinct avian specimens from the Paleogene. However, most specimens still lack well preserved and three-dimensional cranial material, particularly of the palate. Additionally, as remarked by Houde (1988), lithornithids appear to display relatively conservative skeletal morphology across taxa more than five million years apart. With these caveats in mind, we present the following discussion of character states that are variable among lithornithid

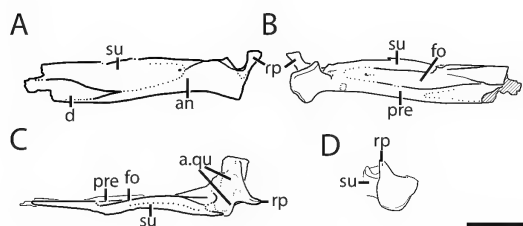


FIG. 35. Posterior portion of the left half of the mandible of the holotype of *Lithornis promiscuus* (USNM 336535) in **A**, lateral, **B**, medial, **C**, dorsal, and **D**, posterior views. Scale = 1 cm. See anatomical abbreviations.

taxa for future analyses. Furthermore, the character states the some lithornithids share with nonlithornithid avians will also be helpful for further testing the relationships of lithornithids.

Character 7. External naris, posterodorsal portion: (0) rounded posterodorsal margin where the nasal is laterally deflected; (1) posteriorly tapered posterodorsal margin where the nasal is dorsoventrally compressed.

The posterodorsal portion of the external naris has a rounded margin bounded by a posterolateral process of the nasal in neognaths (*Gallus gallus*; USNM 19369) and within palaeognaths (*Apteryx owenii*; USNM 18279). In contrast, the posterodorsal portion of the external naris tapers to a point in lateral view in most lithornithids. In this state, the nasal is compressed dorsoventrally and lacks a significant posterolateral process. This state is observed in tinamous (*Crypturellus undulatus*; AMNH 6480) and also in *Pseudocrypturus* (USNM 336103), but is absent in the skull referred to *Lithornis promiscuus* (USNM 391983). Therefore, this character varies within Lithornithidae as well as among other palaeognaths.

Character 17. Cranium, postorbital process: (0) anterodorsally compressed and tapered; (1) broad and rounded so that there is nearly no process (modified from Houde, 1988: 18).

The postorbital process takes two forms in early diverging avians, a small and distinctly

tapered process, or a broader process that is little differentiated from the dorsal skull roof elements. The small and tapered process is present in the proximal outgroups to Aves (e.g., *Archaeopteryx*, *Ichthyornis*), in neognaths (e.g., *Chauna torquata*; AMNH 1773), in most tinamous (e.g., *Crypturellus undulatus*; AMNH 6480) examined by us, and in nearly all lithornithids with well-preserved skulls. The postorbital process is reduced to a poorly projecting knob in ratites (e.g., *Struthio camelus*, USNM 560081). As pointed out by Houde (1988), the largest lithornithid, *Paracathartes howardae* (USNM 361415) has a poorly developed, broad postorbital process like that of ratites.

Character 22. Pterygoid, medial portion anterior to the articulation the basipterygoid process: (0) anteroposterior straight medial margin; (1) distinct, tablike medial expansion.

The medial portion of the pterygoid between the basipterygoid process and the articulation with the palatines has a straight lateral margin in neognaths (e.g., *Gallus gallus*, USNM 19369), *Apteryx owenii* (USNM 18279), and in tinamous (*Timamus major*; USNM 621693). Within palaeognaths, the medial side of the pterygoid is clearly medially expanded as in *Struthio camelus* (USNM 560081) and *Dromaeus novaehollandiae* (TMM unnumbered). In these taxa, the medial expansion forms a depression that opens ventrally and medially. Unfortunately, the condition in the proximal outgroups to Aves is not known. Among lithornithids, expanded medial processes are present in *Lithornis celetius* (USNM 290601), a skull referred to *Lithornis promiscuus* (USNM 391983; fig. 33), a specimen referred to *Lithornis vulturinus* (MGUH 26770), and *Paracathartes howardae* (USNM 391984), but clearly are absent in all of the Green River Formation lithornithids (e.g., *Pseudocrypturus cercanaxius* and *Calciavis grandei*).

Character 25. Palatine, posterior portion, lateral and medial sides framing the posterior portion of the internal choana fossa: (0) wide at posterior portion; (1) converge at an acute point and posterior extent connected to the palate; (2) converge at an acute

point and posterior extent a posteriorly directed process free from connection with the palate. ORDERED.

The palate of palaeognaths has been extremely important for reconstructing relationships at the base of Aves and the interrelationships of Palaeognathae (Huxley, 1867; Bock, 1963; Cracraft, 1974; Houde, 1986, 1988; Lee et al., 1997; Livezey and Zusi, 2006; 2007; Bourdon et al., 2009), and the homology of these character states was previously hotly debated. The morphology of the posterior portion of the palatine where it meets the pterygoid varies across Lithornithidae, and character state changes within the clade also occur among other palaeognaths. Furthermore, the plesiomorphic condition for lithornithids is not clear given that the interrelationships of lithornithids are unresolved. State (0) appears to represent the plesiomorphic condition in Aves but is also present in some lithornithids and some other palaeognaths (e.g., *Struthio camelus*). Nearly all lithornithids (e.g., *Lithornis promiscuus* MGUH 26770) appear to have state (1) where the palatines posteriorly converge to a point and are completely connected with the pterygoid and this character state is also present in *Palaeotis* (Mayr, 2015). *Pseudocrypturus cercanaxius* (holotype), a referred specimen of *Lithornis vulturinus* (Bourdon and Lindow, 2015; MGUH 26770) and tinamous share character state (2) where the palatines posteriorly converge to a point as a small posteriorly projected process that is free from the rest of the palate. Houde (1986; 1988) used the presence of the posteriorly projected process to infer a close relationship between *Pseudocrypturus cercanaxius* and tinamous but hypothesized this was plesiomorphic for palaeognaths.

Character 32. Basicranium, basal tubercles (= basitubera), development on posterolateral regions of basitemporal plate: (0) absent; (1) present (Bertelli and Chiappe, 2005: 3).

The distribution of this character is not clear given that many early diverging avian clades both lack and retain rather large basal tubera

depending on the species-level taxa. Within palaeognaths, significant tubera appear absent in *Rhea americana*, *Dromaeus novaehollandiae*, and tinamous (e.g., *Crypturellus undulatus*; AMNH 6480), but are present in *Apteryx owenii* (USNM 18279), *Emus crassus* (Parker, 1895), and *Struthio* (USNM 560081). Within Lithornithidae, developed tubera are present in *Lithornis celetius* (USNM 290601) and a skull referred to *Lithornis promiscuus* (USNM 391983), are absent in *Paracathartes* (USNM 361415), and appear to be present in a specimen referred to *Lithornis vulturinus* (MGUH 26770).

Character 38. Quadrate, foramen (= caudomedial fossa of Elzanowski and Stidham, 2010) on body: (0) absent; (1) present as either a foramen or deep fossa on posterior surface between the mandibular condyles and the otic process; (2) present as a foramen on the posteromedial surface of the body (modified from Clarke, 2004).

A distinct foramen or a deep fossa on the posterior surface of the quadrate lies between the mandibular condyles and the otic process in *Struthio camelus* (USNM 560081) among palaeognaths and *Gavia immer* (TMM M-unnumbered) among neognaths sampled here, but it is clear the feature is present in some but not all galloanserines (Elzanowski et al., 2001). In lithornithids, a deep fossa is present in the same area in *Lithornis celetius* (USNM 290601), *Lithornis plebius* (USNM 336534), a skull referred to *Lithornis promiscuus* (USNM 391983), *Pseudocrypturus cercanaxius* (USNM 336103), and *Calciavis grandei* (AMNH 30560). A fossa is clearly absent in *Paracathartes howardae* (Houde, 1988).

Character 75. Pygostyle, ventral process: (0) absent; (1) present and pointed; (1) present and club shaped.

Pygostyle morphology was previously used by Houde (1988) to differentiate among his new species of *Lithornis*, particularly *L. promiscuus* and *L. plebius*. We score three morphologies here: taxa with state (0) have no distinct ventral process on the proximoventral portion of the

pygostyle; taxa with state (1) have an anteroventrally directed process that tapers well anteroventral of the articulation with the free caudal vertebrae; and those with state (2) have a ventral process that has a clublike anterodorsal expansion on the proximal termination of the process. In some taxa (e.g., *Paracathartes howardae*, Houde, 1988), the clublike process bears a foramen. The morphology of the ventral process of the pygostyle is thus variable within Lithornithidae, and similar variation is also present in the tinamous species examined for this analysis.

Character 105. Scapula, height of shaft at the proximal end: (0) about twice or less the height of the humeral glenoid; (1) greater than the height of the humeral glenoid.

This character attempts to quantify the size of the articular surface of the scapula for the humerus versus the height of the base of the scapula blade. Among lithornithids, *Paracathartes* (USNM 361419) and *Lithornis promiscuus* (USNM 336535) have proportionally larger articulations for the humerus than the other lithornithids (e.g., *Lithornis celetius*; USNM 290554). Furthermore, the midportion of the scapula blade expands in dorsoventral height relative to the more proximal and distal portions in *Paracathartes* (USNM 361419) and *Lithornis promiscuus* (USNM 336535). A large articulation surface for the humerus of the scapula is also found in a variety of palaeognaths (tinamous, *Rhea*) and neognaths (e.g., *Gallus gallus*) sampled here, suggesting that this character is highly homoplastic.

106. Scapula, distalmost end: (0) blunt or rounded; (1) tapered to a fine point.

The shape of the posterior termination of the scapula blade varies across the early diverging avians sampled here and throughout Aves. In most forms, the scapula blade gradually tapers posteriorly and terminates in a fine point. This is also true of nearly all the lithornithids sampled here. In contrast, all the Green River Formation lithornithids that could be scored have a scapula

blade that terminates in a blunt and slightly rounded form.

Character 143. Metacarpal III, proximal portion, ventral side: (0) smooth or very slight expansion; (1) distinct tuber present.

The ventral surface of the proximal portion of metacarpal III bears a well-developed tuber (Houde, 1988) in most lithornithids, including *Lithornis promiscuus* (USNM 336535), *Lithornis plebius* (USNM 336534), *Calciavis grandei* (AMNH 30578), and a referred specimen of *Lithornis celetius* (Houde, 1988). A tuber is clearly absent in the same location in *Paracathartes howardae* (USNM 361446) and most other Aves with the exception of the extinct galliform *Gallinuloides wyomingensis* (WDC CGR-012). A similarly positioned, but poorly developed tuber is also present in *Iaceornis marshi* (YPM 1734; Clarke, 2004).

Character 151. Ilium, antitrochanter, posterior extent in lateral view: (0) anterior portion of articulation between the ilium and ischium visible; (1) posterior extent of the antitrochanter hides the anterior portion of ilioischiatric fenestra.

The lateral expansion of the antitrochanter of the ilium is variable across Aves. In taxa scored as state (0), the lateral apex of the antitrochanter projects laterally and does not expand posteriorly to obscure the junction between the ilium and the ischium in lateral view. In taxa scored as state (1), the lateral apex of the antitrochanter is shifted posteriorly, so nearly all of the ilium and ischium contact is covered in lateral view. Both character states are widely distributed across the taxa sampled in this analysis, thus suggesting these character states are homoplastic even within sampled subclades (e.g., tinamous). Nevertheless, the character is variable within lithornithids; *Lithornis plebius* (USNM 336534) and a specimen referred to *L. vulturinus* (MGUH 26770) are scored as state (0), whereas *Lithornis promiscuus* is scored as state (1).

Character 154. Pubis, preacetabular pectineal process: (0) absent; (1) present and small flange; (2)

present as a well-developed flange. ORDERED (Clarke et al., 2006: 159).

The size of the preacetabular pectineal process of the pubis varies in early-diverging avians from a slight change in angle (considered absent here) to an elongated, anteroventrally directed finger-like process. Among palaeognaths, a well-developed flange (state 2) is present in *Struthio* (USNM 560081), *Apteryx owenii* (USNM 18279), and all tinamous (e.g., *Eudromia elegans* USNM 345096). In most lithornithids, the pectineal process is present and developed as a distinct, but poorly expanded flange (e.g., *Lithornis promiscuus*, USNM 336535). However, in *Lithornis celestius* (USNM 290601), the pectineal process of the pubis is more elongate and more like that of some tinamous (Houde, 1988).

Character 156. Ischium, distal portion: (0) same width or expanded posteriorly; (1) tapers posteriorly.

The ischium of most basal Aves sampled in this analysis is dorsoventrally tall and terminated abruptly distally. In lithornithids, the posterior portion of the ischium is rarely preserved, but in *Lithornis plebius* (USNM 336534), the ischium gradually tapers to a thin point posteriorly. In *Calciavis grandei* (AMNH 30578), the posterior portion of the ischium terminates abruptly like that of other palaeognaths.

180. Tarsometatarsus: trochlea II, distal extent of trochlea II relative to trochlea IV: (0) approximately equal in distal extent; (1) trochlea II shorter than trochlea IV, but reaching distally further than base of trochlea IV trochlea; (2) trochlea II shorter than trochlea IV, reaching distally only as far as the base of trochlea IV. ORDERED (Clarke et al., 2006: 205).

The extent of the tarsometatarsal trochlea has been used widely in avian phylogenetics and character state changes are common among basal avians. Nearly all the lithornithids scored here have an asymmetrical distal portion of the tarsometatarsal where the trochlea II is shorter than that of trochlea IV. In contrast, all of the Green

River Formation lithornithid specimens including *Calciavis grandei* and *Pseudocrypturus cercanaxius* have a symmetrical distal portion of the tarsometatarsus with trochleae II and IV subequal in distal extent.

RELATIONSHIPS OF LITHORNITHIDAE

The relationships of Paleogene palaeognaths from North America were first tackled by Houde and Olson (1981) and Houde (1986). In a monograph that soon followed, Houde (1988) named three species of *Lithornis* (*L. promiscuus*, *L. plebius*, and *L. celestius*), named a closely related form *Pseudocrypturus cercanaxius* from the Green River Formation, referred a partial skeleton of a *Lithornis*-like taxon to *Paracathartes howardae*, revised *Lithornis* taxa from Europe, and hypothesized and detailed the relationships of these taxa to palaeognaths. Houde (1988) hypothesized that *Lithornis*, *Pseudocrypturus cercanaxius*, and *Paracathartes howardae* represented successive outgroups to extant ratites based on hand-drawn character optimizations (Tinamidae were considered neognaths in that analysis). Houde (1988) presented alternative hypotheses of the relationships of *Lithornis*, *Pseudocrypturus cercanaxius*, and *Paracathartes howardae*, but none included a monophyletic group consisting of all three taxa without any extant ratites. Houde (1988) elaborated, however, on the potential character optimization of features of lithornithids among basal avians. Later analyses of lithornithid relationships included supraspecific genus-level terminal taxa (e.g., *Lithornis*; Dyke, 2003; Clarke, 2004; Livezey and Zusi, 2006; 2007; Johnston, 2011). In all these analyses except that of Livezey and Zusi (2006; 2007), *Lithornis* was found within Palaeognathae with few palaeognaths sampled (Clarke, 2004), as the sister taxon of extant ratites (Dyke, 2003), and as a ratite as the sister taxon of Tinamidae (Johnston, 2011).

Other than Houde's (1988) analysis, all subsequent analyses did not specifically address the relationships of distinct species of lithornithids,

and variation in character states among potential members of Lithornithidae was not addressed. The analysis of Houde (1988) included discussion of differences among lithornithids, specifically *Lithornis*, *Pseudocrypturus cercanaxius*, and *Paracathartes howardae*. However, the discussions of optimizations have drastically changed since Houde's (1988) study.

Relationships at the base of Aves, including a monophyletic Palaeognathae (containing ratites and Tinamidae) and Neognathae (containing Galloanserae and Neoaves) are well supported. Nevertheless, the relationships among Palaeognathae are far from resolved and continue to be a problem when reconstructing relationships from either morphology and/or molecular data (see Bourdon et al., 2009; Hackett et al., 2008; Phillips et al., 2010; Johnston, 2011; Haddrath and Baker, 2012; Baker et al., 2014; Mitchell et al., 2014). Moreover, nearly every possible relationship among palaeognaths has been suggested and supported by at least some data. In this context, we treat our limited osteology-only analyses with caution and understand it to be only one further contribution to an ongoing conversation on the evolution of morphology in Palaeognathae. Rather than proposing our results as definitive, we propose that only more-inclusive molecular, possibly genome-scale phylogenies of palaeognaths and more-inclusive analyses with all fossil taxa can approach this question with more confidence. Specifically, we focused our analysis at investigating the character optimizations among lithornithid taxa as presented by Houde (1988) using the morphological data extracted from the complete and partial specimens from the Green River Formation. Integration of these data resulted in a monophyletic Lithornithidae as the sister taxon of Tinamidae within Palaeognathae in the unconstrained analyses. A Lithornithidae-Tinamidae clade, placed at the base of Palaeognathae is supported in both the "total" and "core lithornithid" analysis by the following list of unambiguously optimized apomorphies:

(1) maxillopalatine antrum absent (C4:0);

- (2) frontal-parietal suture open (C12:0);
- (3) extensive contact between the lacrimal and ectethmoid (C16:1);
- (4) cluster of pneumatic foramina on the posterior surface of the otic head of the quadrate (C43:1);
- (5) small horizontal shelf at the posterior portion of the mandibular symphysis (C48:1);
- (6) corpus of the axis with pneumatic foramina on lateral sides (C62:1);
- (7) acromion of the scapula projected anteriorly to surpass the articular surface for coracoid (tuberculum coracoidei of Baumel and Witmer, 1993) (C103:0);
- (8) pneumatic foramina within of pneumotricipital fossa of the humerus (C111:1);
- (9) intermetacarpal space (between metacarpals II and III) terminates distal to metacarpal I (C141:1);
- (10) manual digit III, phalanx 1, length less than 50% the length of digit II, phalanx 1 (C146:1);
- (11) plantar surface of the tarsometatarsus trochlea II and IV expanded into distinct "wings" (C177:1).

Out of this list of apomorphies and the taxa sampled here, two apomorphies (extensive contact between the lacrimal and ectethmoid C16:1; small horizontal shelf at the posterior portion of the mandibular symphysis C48:1) were present exclusively in Lithornithidae and Tinamidae. Furthermore, two other apomorphies also are clearly present in Lithornithidae and Tinamidae among Palaeognathae (manual digit III, phalanx 1, length less than 50% the length of digit II, phalanx 1 [C146:1]; plantar surface of the tarsometatarsus trochlea II and IV expanded into distinct "wings" [C177:1] [also in *Apteryx owenii*]) but also present in some of the sampled neognaths. However, some unambiguous characters supporting this clade (C4:0, C12:0, C62:1, C103:0) likely represent plesiomorphies for Palaeognathae or even Aves based on other phylogenetic analyses of early avian lineages (e.g., Clarke, 2004). Furthermore, forelimb character states optimized as Lithornithidae-Tinamidae apomor-

phies (C111:1, C141:1, C146:1) are difficult to score in ratites with reduced forelimbs. In sum, the Bremer support of the Lithornithidae-Tinamidae clade is relatively high compared to other subclades, but on closer examination a number of the characters identified as supporting the relationship within the scope of our analysis are likely to be plesiomorphic or homoplastic at a broader scope.

Other evidence has been proposed to suggest a close relationship between Lithornithidae and Tinamidae. For example, an analysis examining tinamou eggshell microstructure (Grellet-Tinner and Dyke, 2005) and eggshell attributed to two lithornithids species (*Lithornis vulturinus* and *Lithornis celetius*) suggested that the microstructure of tinamous and lithornithid eggs are more similar to each other than those of ratites. Furthermore, Houde (1988) hypothesized that lithornithids exclusively shared a diminutive caudal series with tinamous, but at the time did not have any complete caudal series of any lithornithid. The complete caudal series of the holotype of *Calciavis grandei* (AMNH 30578) confirms Houde's (1988) statement. However, it is worth noting that the caudal series is weakly developed with diminutive transverse processes in all ratites; a similarly tiny pygostyle is also common and these morphologies are thus not unique to tinamous and lithornithids (Clarke, 2002; Bertelli et al., 2014). In an analysis of the relationships of palaeognaths based on the morphology of the palate, Johnston (2011) found a sister-taxon relationship between *Lithornis* and Tinamidae citing one apomorphy, palatine lateral border directed at midline rostral to basipterygoid articulation (Johnston, 2011: char. 17). Dyke and van Tuinen (2004) and Leonard et al. (2005) reported the placement of lithornithids (as the sister taxon to tinamous), and indicated this was recovered through analysis, but the associated data set yielding this result was never published. The data set of Dyke (2003) which appears to form the basis for these analyses does not yield the tree reported and scores characters from specimens not preserving the relevant morphologies (Mayr, 2009).

A Tinamou + Lithornithidae clade, if supported in more inclusive analyses, would have implications for the evolution of tinamous, the only comparatively species-rich clade of palaeognaths so far only represented by a small number extinct forms (Bertelli and Chiappe, 2005; Bertelli et al., 2014). The earliest lithornithids possibly appear in the Paleocene of Europe (e.g., *Fissuravis*) and are in North America by the Paleocene (Houde, 1988; Stidham et al., 2014), whereas the first tinamous appear in the Miocene of Argentina (Bertelli and Chiappe, 2005; Bertelli et al., 2014). These data have two important implications. First, it is possible that the tinamous total group including lithornithids originated in North America and retracted to their current Neotropical biogeographic distribution from the Paleogene to the Neogene. This pattern would be somewhat similar to other avian subclades with stem members in Paleogene of North America and Europe and a southern extant distribution across former parts of Gondwanan continents (e.g., Steatornithidae, Mayr, 2005; Coracii, Clarke et al., 2009; Coliiformes, Ksepka and Clarke, 2009; Podargiformes, Nesbitt et al., 2011). Second, tinamous may have diverged from other palaeognaths more recently and their crown diversification could be in the Miocene closer to their first fossil records (Bertelli and Chiappe, 2005).

Results constraining the analysis to take into account abundant data from molecular data from nuclear to mitochondrial gene sequence data and including assessment of retroelement insertions and ultraconserved elements (e.g., Phillips et al., 2010; Haddrath and Baker, 2012; Baker et al., 2014; Mitchell et al., 2014) are consistent with a different picture of early palaeognath evolution (figs. 29–31). In all these analyses, Lithornithidae is not recovered with Tinamidae (now well nested within the large flightless ratites) but is again placed at the base of the Palaeognathae. If this topology is correct, the unconstrained analysis may differ because that analysis is influenced by the

flight-related characters in the clade, recovering a single loss in a monophyletic Ratitae of traits in the outgroups. Once tinamous are nested within a paraphyletic ratite assemblage in the constrained analyses, flight characters become ambiguously optimized (present in Neognathae, outgroups, and Palaeognathae). Recent phylogenies of extinct and extant palaeognaths (not sampling lithornithids) have painted a complex biogeographical picture largely inconsistent with a single loss of flight and rafting of already flightless taxa during Gondwanan breakup (e.g., Baker et al., 2014; Mitchell et al., 2014). Consistent placement of the volant Lithornithidae at the base of the clade suggests they could yield further insight into the plesiomorphic morphologies for a total group that has apparently lost flight repeatedly and dispersed broadly.

PERSPECTIVES

Species relationships in Lithornithidae vary depending upon their placement in Palaeognathae. Morphological diversity in Lithornithidae should not be underestimated, and therefore, species terminals should be used in future phylogenetic analyses addressing basal Aves and Palaeognathae. Resolution of palaeognath relationships likely will require even larger data sets and comprehensive reassessment of all morphological diversity in the clade, which was not undertaken here. Other recent analyses using data sets including different morphological (e.g., Worthy and Scofield, 2012; Bertelli et al., 2014) or molecular sequence data sets (Baker et al., 2014; Mitchell et al., 2014) recover distinct palaeognath relationships from each other and from the analyses presented here. The character data made available here, however, critically inform evaluation of one of the best-represented extinct clades in Palaeognathae and contribute to this broader enterprise of integrating data on osteology, soft tissue, behavior, and reproductive systems with molecular sequence data to further illuminate character evolution in the clade.

ACKNOWLEDGMENTS

We want to thank Mark Norell (AMNH), Lance Grande, and Peter Makovicky (FMNH) for making this comprehensive project possible. Rick Edwards (AMNH) photographed AMNH 30578 and preparation of the specimen was finished by Marilyn Fox (YPM). Christopher Torres and Daniel Lawver contributed measurement data and other insights into the anatomy of the new species. Discussions with Dan Ksepka, Nathan Smith, Daniel Lawver, and Christopher Torres greatly improved the manuscript. We also thank William Simpson (FMNH), Helen James (USNM), and Mark Florence (USNM), Sandra Chapman (NHMUK), and Carl Mehling (AMNH) for assisting us with access to specimens. This project was made possible by National Science Foundation grants: “Integrated study of an exceptional avifauna from the Eocene Green River Formation: new data on avian evolution and taphonomy” (EAR 0719758) and “Collaborative Research: Phylogenomics of palaeognathous birds and understanding the evolution of flightlessness” (EAR 1355292) to J.A.C. We thank two anonymous reviewers for the critical comments on the anatomy and phylogeny that greatly improved the manuscript.

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APPENDIX 1

PHYLOGENETIC CHARACTERS AND SCORES
CHARACTERS

1. Premaxillae: (0) fused anteriorly in adults, posterior nasal [frontal] processes not fused to each other; (1) frontal processes completely fused as well as anterior premaxillae (Clarke et al., 2006: 1).
2. Premaxilla, pair of distinct furrows anterior to the external naris: (0) absent; (1) present (modified from Mayr and Clarke, 2003: 4).
3. Maxillary teeth: (0) present; (1) absent (Clarke et al., 2006: 4).
4. Maxilla, maxillopalatine antrum: (0) absent; (1) present as a "large pocket" formed from the maxillopalatines, the anterior margin ankylosing with the posterior margin of the maxillary (modified from Lee et al., 1997: 57).
5. Maxilla, height of lateral portion ventral to antorbital fenestra (subnarial rostrum) in lateral view: (0) dorsoventrally expanded above horizontal plane as the attached palatal elements; (1) similar height (in the same horizontal plane) as the attached palatal elements, dorsoventrally thin.
6. Facial margin: (0) maxillary process of the premaxilla extending less than 1/2 facial margin; (1) maxillary process of the premaxilla extending more than 1/2 of facial margin (Clarke et al., 2006: 9).
7. External naris, posterodorsal portion: (0) rounded posterodorsal margin where the nasal is laterally deflected; (1) posteriorly tapered posterodorsal margin where the nasal is dorsoventrally compressed.
8. Osseous interorbital septum (= mesethmoid), exposure on the skull roof: (0) absent; (1) present (Craft, 1974).
9. Osseous interorbital septum (= mesethmoid): (0) restricted to posterior or another just surpassing premaxillae/frontal contact in rostral extent does not surpass posterior edge of external nares in rostral extent; (1) extending rostral to posterior extent of frontal processes of premaxillae and rostral to posterior edge of external nares (Clarke et al., 2006: 27).
10. Olfactory chamber: (0) ossification of chamber absent or relatively poorly developed; (1) ossification of chamber well developed (Lee et al., 1997: 58).
11. Nasal-frontal articulation area, at the midline: (0) nearly flat; (1) depression present.
12. Frontal-parietal suture, dorsal surface: (0) open; (1) fused (Clarke et al., 2006: 52).
13. Lacrimal, ventral process, lateral exposure: (0) anteroposteriorly thin, blade-like; (1) broad, flat laterally.
14. Lacrimal, ventral process: (0) short and does not touch the jugal; (1) well developed and touches or nearly touches the jugal bar (modified from Mayr and Clarke, 2003: 12).
15. Lacrimal, elongated supraorbital process, projecting posterolaterally over the orbit: (0) absent; (1) present (Lee et al., 1997: 52).
16. Cranium, ectethmoid: (0) does not contact lacrimal; (1) extensive contact with lacrimal (modified from Bertelli and Chiappe, 2005: 5).
17. Cranium, postorbital process: (0) anterodorsally compressed and tapered; (1) broad and rounded, so that there is nearly no process (modified from Houde, 1988: 18).
18. Skull length versus humerus: (0) humerus longer or the same length; (1) skull longer.
19. Palatines-ptyergoid: (0) separate elements; (1) fused (Mayr and Clarke, 2003).
20. Ptyergoid-palatine articulation area, lateral side: (0) smooth; (1) distinct fossa present without dorsally bounding ridge; (2) distinct fossa present with dorsally bounding ridge. ORDERED.
21. Palatine and ptyergoid: (0) long, anteroposteriorly overlapping, contact; (1) short, primarily dorsoventral, contact (Clarke et al., 2006: 16).
22. Ptyergoid, medial portion anterior to the articulation the basiptyergoid process: (0) anteroposterior straight medial margin; (1) distinct, tablike medial expansion.
23. Ptyergoid, ventral surface anterior to the articulation with the basiptyergoid processes, ventromedially opening fossa: (0) absent; (1) present (modified from Lee et al., 1997: 54).
24. Ptyergoid-vomer, articulation: (0) present, well developed; (1) reduced, narrow process of ptyergoid passes dorsally over palatine to contact vomer; (2) absent, ptyergoid and vomer do not contact (Clarke et al., 2006: 15).
25. Palatine, posterior portion, lateral and medial sides framing the posterior portion of the internal chaona fossa: (0) wide at posterior portion; (1) converge at an acute point and posterior extent connected to the palate; (2) converging at an acute point and posterior extent a posteriorly directed process free from connection with the palate. ORDERED.
26. Vomer-premaxilla contact: (0) present; (1) absent (Clarke et al., 2006: 18).
27. Basiptyergoid processes, lateral expansion: (0) long; (1) short (articulation with ptyergoid subequal to or longer than amount projected from the basisphenoid rostrum) (modified from Clarke et al., 2006: 21).
28. Basisphenoid-ptyergoid articulations: (0) located on the posterior portion of the basisphenoid; (1)

- located markedly anterior on basisphenoid (parasphenoid rostrum) such that the articulations are subadjacent on the narrow rostrum (Clarke et al., 2006: 22).
29. Basisphenoid-pterygoid articulation, orientation of contact: (0) mediolateral; (1) entirely dorsoventral (Clarke et al., 2006: 23).
 30. Pterygoid, articular surface for basisphenoid: (0) flat to convex; (1) flat to convex facet, stalked, variably projected (Clarke et al., 2006: 24).
 31. Opisthotic/prootic, pila otica: (0) without cluster of small pneumatic openings; (1) with cluster of small pneumatic openings (modified from Mayr and Clarke, 2003: 31).
 32. Basicranium, basal tubercles (= basitubera), development on posterolateral regions of basitemporal plate: (0) absent; (1) present (Bertelli and Chiappe, 2005: 3).
 33. Occipital condyle, size: (0) large (1/3+ width of width of foramen magnum); (1) tiny.
 34. Eustachian tubes: (0) paired and lateral; (1) paired, close to midline; (2) paired and adjacent on midline or single anterior opening (Clarke et al., 2006: 28).
 35. Squamosal, ventral or "zygomatic" process: (0) variably elongate, dorsally enclosing otic process of the quadrate and extending anteroventrally along shaft of this bone, dorsal head of quadrate not visible in lateral view; (1) short, head of quadrate exposed in lateral view (Clarke et al., 2006: 30).
 36. Quadrate-pterygoid contact: (0) as a facet, variably with slight anteromedial projection cradling base; (1) condylar, with a well-projected tubercle on the quadrate (Clarke et al., 2006: 33).
 37. Quadrate, well-developed tubercle on anterior surface of dorsal process: (0) absent; (1) present (Clarke et al., 2006: 34).
 38. Quadrate, foramen on body: (0) absent; (1) present as either a foramen (= foramen pneumaticum rostromediale of Elzanowski and Stidham, 2010) or deep fossa on posterior surface between the ventral condyles and the otic process; (2) present as a foramen on the posteromedial surface of the body (modified from Clarke, 2004).
 39. Quadrate, orbital process: (0) pterygoid articulation does not reach tip; (1) pterygoid articulation with no extent up orbital process, restricted to quadrate (Clarke et al., 2006: 32).
 40. Quadrate, orbital process: (0) tapers anteriorly; (1) anterior end dorsoventrally expanded.
 41. Quadrate, length of the orbital process: (0) long, about the length of the body; (1) short, hatchet shaped, significantly shorter than the length of the body.
 42. Quadrate, dorsal process, development of intercotylar incisure between prootic and squamosal cotylae: (0) absent, articular surfaces not differentiated; (1) two distinct articular facets, incisure not developed (Clarke et al., 2006: 37).
 43. Quadrate, cluster of pneumatic foramina on the posterior surface of the otic process: (0) absent; (1) present (Clarke et al., 2006: 44).
 44. Quadrate, mandibular articulation: (0) bicondylar articulation with mandible; (1) tricondylar articulation, additional posterior condyle or broad surface (Clarke et al., 2006: 38).
 45. Quadrate, ventral portion, intercondylar fossa: (0) shallow; (1) deep, rounded pit (Lee et al., 1997: 55).
 46. Quadrate, pneumatization, large, single pneumatic foramen: (0) absent; (1) posteromedial surface of corpus (Clarke et al., 2006: 41).
 47. Dentaries: (0) joined proximally by ligaments; (1) joined by bone (Clarke et al., 2006: 7).
 48. Mandibular symphysis, posterior portion, small horizontal shelf: (0) absent; (1) present.
 49. Mandibular symphysis, two strong grooves forming an anteriorly opening "V" in ventral view: (0) absent; (1) present (Clarke et al., 2006: 8).
 50. Mandibular symphysis, anterior occlusal portion (dorsal surface): (0) more than one row of foramina; (1) a single row of foramina.
 51. Mandibular symphysis, anteroposteriorly extensive, flat to convex, dorsal-facing surface developed: (0) absent, concave; (1) flat surface developed (Clarke et al., 2006: 45).
 52. Mandibular symphysis, symphyseal foramen/foramina: (0) single; (1) paired (Clarke et al., 2006: 47).
 53. Mandibular symphysis, symphyseal foramen/foramina: (0) opening on posterior edge of symphysis; (1) opening on dorsal surface of symphysis (Clarke et al., 2006: 48).
 54. Dentary teeth: (0) present; (1) absent (Clarke et al., 2006: 5).
 55. Dentary, posterior portion: (0) unforked, or with a weakly developed dorsal ramus; (1) strongly forked with the dorsal and ventral rami approximately equal in posterior extent (Clarke et al., 2006: 43).
 56. Coronoid ossification: (0) present; (1) absent (Clarke et al., 2006: 19).
 57. Splenial, anterior extent: (0) splenial stops well posterior to mandibular symphysis; (1) extending to mandibular symphysis, though not contacting; (2) extending to proximal tip of mandible, contacting on midline. ORDERED (Clarke et al., 2006: 44).
 58. Mandible, long and strongly mediolaterally compressed retroarticular process: (0) absent; (1) present (Mayr and Clarke, 2003: 44).

59. Mandible, dorsal view, medial mandibular process and development of posterior cotyla: (0) broad process of triangular outline and a well-developed posterior cotyla that connects to lateral cotyla; (1) triangular process and a posterior cotyla separated from lateral cotyla; (2) elongated process and poorly developed posterior cotyla; (3) narrow and very elongated process and reduced or absent posterior cotyla. ORDERED (Bertelli and Chiappe, 2005: 10).
60. Mandible, articular region, area immediately posterior to articular facets for the quadrate (= retroarticular process): (0) absent or poorly expanded dorsally; (1) expanded posterodorsally as a short, fingerlike process.
61. Mandible, medial process: (0) short and directed medially; (1) long, narrow, and dorsally oriented (modified from Mayr and Clarke, 2003: 45).
62. Axis, corpus with pneumatic foramina on lateral sides: (0) absent; (1) present (Mayr and Clarke, 2003: 48).
63. Axis, transverse foramina: (0) present; (1) absent (Mayr and Clarke, 2003: 49).
64. Third cervical vertebra, osseous bridge from the transverse process to the postzygapophysis that forms a foramen in dorsal view: (0) absent; (1) present (Mayr and Clarke, 2003: 52).
65. Cervical vertebrae: (0) variably dorsoventrally compressed, amphicoelous ("biconcave"): flat to concave articular surfaces; (1) anterior surface heterocoelous (i.e., mediolaterally concave, dorsoventrally convex), posterior surface flat; (2) heterocoelous anterior (i.e., mediolaterally concave, dorsoventrally convex) and posterior (i.e., mediolaterally convex, dorsoventrally concave) surfaces. ORDERED (Clarke et al., 2006: 53).
66. Thoracic vertebrae: (0) at least part of series with subround, central articular surfaces (e.g., amphicoelous/opisthocoelous) that lack the dorsoventral compression seen in heterocoelous vertebrae; (1) series completely heterocoelous (Clarke et al., 2006: char. 56).
67. Thoracic vertebrae, lateral surfaces of centra: (0) flat to slightly depressed; (1) deep, emarginated fossae; (2) central ovoid foramina (Clarke et al., 2006: char. 59).
68. Notarium: (0) absent; (1) present and composed of three vertebrae; (2) present and composed of four vertebrae or more. ORDERED (Bertelli and Chiappe, 2005: 11).
69. Sacral vertebrae, number ankylosed: (0) 10 or less; (1) 11–14; (2) 15 or more. ORDERED (Clarke et al., 2006: 61).
70. Sacral vertebrae, series of short vertebrae, with dorsally directed parapophyses just anterior to the acetabulum: (0) absent; (1) present, three such vertebrae; (2) present, four such vertebrae. ORDERED (Clarke et al., 2006: 63).
71. Caudal vertebrae, chevrons, fused on at least one anterior caudal: (0) present; (1) absent (Clarke et al., 2006: 65).
72. Free caudal vertebrae, length of transverse processes: (0) subequal or longer than the width of centrum; (1) significantly shorter than centrum width (Clarke et al., 2006: 66).
73. Anterior free caudal vertebrae: (0) pre- and postzygapophyses short and variably noncontacting; (1) prezygapophyses clasping the posterior surface of neural arch of preceding vertebra, postzygapophyses negligible (Clarke et al., 2006: 67).
74. Fused distal caudal vertebrae, morphology: (0) length greater than two caudal vertebrae; (1) less than or equal to two caudal vertebrae in length (Clarke et al., 2006: 69).
75. Pygostyle, ventral process: (0) absent; (1) present and pointed; (2) present and club shaped.
76. Pygostyle, corpus perforated by foramen at posteroventral end: (0) absent; (1) present (Mayr and Clarke, 2003: 61).
77. Ossified uncinat processes: (0) unfused to ribs; (1) fused to ribs (Clarke et al., 2006: 70).
78. Sternum, pneumatic foramina in the depressions (loculi costalis; Baumel and Witmer, 1993) between rib articulations (processi articularis sternocostalis; Baumel and Witmer, 1993): (0) absent; (1) present (Clarke et al., 2006: 75).
79. Sternum, coracoidal sulci spacing on anterior edge: (0) adjacent; (1) crossed on midline; (2) displaced laterally, not touching on the midline (Clarke et al., 2006: 76).
80. Sternum, lateral view: (0) moderate to highly curved; (1) flattened (Lee et al., 1997: 5).
81. Sternum, number of processes for articulation with the sternal ribs: (0) four or less; (1) five; (2) six; (3) seven or more. ORDERED (modified from Clarke et al., 2006: 76).
82. Sternum, raised, paired intermuscular ridges (linea intermuscularis; Baumel and Witmer, 1993) parallel to sternal midline: (0) absent; (1) present (Clarke et al., 2006: 78).
83. Sternum, posterior margin, distinct posteriorly projected medial and/or lateral processes: (0) absent (directly laterally projected zyphoid processes developed, but not considered homologues as these are copresent with the posterior processes in the new clade); (1) with distinct posterior processes; (2) midpoint of posterior sternal margin connected to medial posterior processes to enclose

- paired fenestra. ORDERED (Clarke et al., 2006: 79).
84. Sternum, keel: (0) present; (1) absent (Cracraft, 1974).
 85. Sternum, posterior notch(es): (0) shallow, less than half the length of the sternum; (1) deep, greater than half the length of the sternum.
 86. Furcula, hypocleideum: (0) absent; (1) a tubercle; (2) an elongate process. ORDERED (Clarke et al., 2006: 82).
 87. Furcula, dorsal (omal) tip: (0) flat or blunt tip; (1) with a pronounced posteriorly pointed tip (Clarke et al., 2006: 84).
 88. Furcula, ventral margin of apophysis: (0) curved, angling; (1) with a truncate or squared base (Clarke et al., 2006: 85).
 89. Scapula-coracoid articulation: (0) pit-shaped scapular cotyla developed on the coracoid, and coracoidai coracoidal tubercle developed on the scapula ("ball and socket" articulation); (1) flat (Clarke et al., 2006: 87).
 90. Coracoid and scapula: (0) separate elements; (1) fused (Mayr and Clarke, 2003: 68).
 91. Coracoid, procoracoid process: (0) absent; (1) present (Clarke et al., 2006: 88).
 92. Coracoid, dorsal surface (= posterior surface of early diverging maniraptoran theropods): (0) strongly concave; (1) flat to convex (Clarke et al., 2006: 91).
 93. Coracoid, pneumatized: (0) absent; (1) present (Clarke et al., 2006: 92).
 94. Coracoid, pneumatic foramen on the dorsal surface of the distal end (near articulation with the sternum): (0) absent; (1) present (Clarke et al., 2006: 93).
 95. Coracoid, posteroventral surface to the hooked acrocoracoid process: (0) smooth; (1) foramina present.
 96. Coracoid, lateral process: (0) absent; (1) present (Clarke et al., 2006: 94).
 97. Coracoid, ventral surface, lateral intermuscular line or ridge: (0) absent; (1) present (Clarke et al., 2006: 95).
 98. Coracoid, acrocoracoid: (0) straight; (1) hooked medially (Clarke et al., 2006: 97).
 99. Coracoid, n. supracoracoideus passes through coracoid: (0) present; (1) absent (Clarke et al., 2006: 98).
 100. Coracoid, medial surface, area of the foramen n. supracoracoideus (when developed): (0) strongly depressed; (1) flat to convex (Clarke et al., 2006: 99).
 101. Coracoid, proximal end, large foramen located on dorsal surface, just distal to the articular surface for the scapula, development: (0) not excavated; (1) large opening (modified from Bertelli and Chiappe, 2005: 18). Only tinamous are scored as applicable here.
 102. Scapula, length: (0) shorter than humerus; (1) as long as or longer than the humerus (Clarke et al., 2006: 103).
 103. Scapula, acromion: (0) projected anteriorly to surpass the articular surface for coracoid (tuberculum coracoidei; Baumel and Witmer, 1993); (1) projected less anteriorly than the articular surface for coracoid (Clarke et al., 2006: 104).
 104. Scapula, acromion: (0) straight; (1) laterally hooked tip without small foramina on the posterior side; (2) laterally hooked tip with small foramina on the posterior side. ORDERED (modified from Clarke et al., 2006: 105).
 105. Scapula, height of shaft at the proximal end: (0) about twice or less the height of the humeral glenoid; (1) greater than the height of the humeral glenoid.
 106. Scapula, distalmost end: (0) blunt or rounded; (1) tapered to a fine point.
 107. Humerus and ulna, length: (0) humerus longer than ulna; (1) ulna and humerus approximately the same length; (2) ulna significantly longer than humerus. ORDERED (Clarke et al., 2006: 106).
 108. Humerus, capital groove: (0) an open groove; (1) closed by tubercle associated with a muscle insertion just distal to humeral head (Clarke et al., 2006: 110).
 109. Humerus, ventral tubercle, proximal extent compared with the head: (0) more distal or equal to the than the distal portion of the head; (1) well within the head; (2) at the proximal portion or more proximal (modified from Lee et al., 1997: 12).
 110. Humerus, proximal end, one or more pneumatic foramina: (0) absent; (1) present (Clarke et al., 2006: 120).
 111. Humerus, pneumatic foramina within the pneumotricipitalis fossa: (0) absent; (1) present (Mayr and Clarke 2003: 77).
 112. Humerus, transverse ligament sulcus: (0) deep; (1) shallow (Clarke 2004: 111).
 113. Humerus, deltopectoral crest: (0) projected dorsally (in line with the long axis of humeral head); (1) projected anteriorly (Clarke et al., 2006: 113).
 114. Humerus, deltopectoral crest: (0) less than shaft width; (1) same width (Clarke et al., 2006: 114).
 115. Humerus, deltopectoral crest, proximoposterior surface: (0) flat to convex; (1) concave (Clarke et al., 2006: 115).
 116. Humerus, deltopectoral crest: (0) pronounced and arcuate; (1) reduced and proximally localized to less than 1/3 the length of the humerus (Houde, 1988: 32).

117. Humerus, deltopectoral crest, distal end in dorsal view: (0) steep angle relative to the shaft; (1) low angle relative to the shaft.
118. Humerus, bicipital crest, pit-shaped fossa for muscular attachment: (0) anterodistal on bicipital crest; (1) directly ventrodistal at tip of bicipital crest; (2) posterodistal, variably developed as a fossa; (3) posterodistal, variably developed as a fossa with a hook-shaped extension. ORDERED (Clarke et al., 2006: 118).
119. Humerus, bicipital crest: (0) little or no anterior projection; (1) developed as an anterior projection relative to shaft surface in ventral view; (2) hypertrophied, rounded tumescence. ORDERED (Clarke et al., 2006: 119).
120. Humerus, distal end, long axis of dorsal condyle: (0) at low angle to humeral axis, proximodistally orientated; (1) at high angle to humeral axis, almost transversely orientated (Clarke et al., 2006: 122).
121. Humerus, distal condyles: (0) subround, bulbous; (1) weakly defined, "straplike" (Clarke et al., 2006: 123).
122. Humerus, distal margin: (0) approximately perpendicular to long axis of humeral shaft; (1) ventrodistal margin projected significantly distal to dorsodistal margin, distal margin angling strongly ventrally (sometimes described as a well-projected flexor process) (Clarke et al., 2006: 124).
123. Humerus, distal end, compressed anteroposteriorly and flared dorsoventrally: (0) absent; (1) present (Clarke et al., 2006: 125).
124. Humerus, distal end, brachial fossa: (0) absent; (1) present, developed as a flat scar or as a scar-impressed fossa. (Clarke et al., 2006: 126).
125. Humerus, distal end, ventral condyle: (0) length of long axis of condyle less than the same measure of the dorsal condyle; (1) same or greater (Clarke et al., 2006: 127).
126. Humerus, distal end, dorsal tuber: (0) absent or short; (1) greatly elongated proximodistally (Mayr and Clarke, 2003: 76).
127. Humerus, distal end, demarcation of muscle origins (e.g., m. extensor metacarpi radialis in Aves) on the dorsal edge: (0) no indication of origin as a scar, pit, or tubercle; (1) indication as a pit-shaped scar or as a variably projected scar-bearing tubercle or facet (Clarke et al., 2006: 128).
128. Humerus, distal end, posterior surface, groove for passage of m. scapulotriceps: (0) absent; (1) present (Clarke et al., 2006: 129).
129. Ulna, proximal portion, bicipital scar: (0) developed as a slightly raised scar; (1) developed as a conspicuous tubercle (Clarke et al., 2006: 135).
130. Ulna, distal end, dorsal condyle, dorsal trochlear surface, extent along posterior margin: (0) less than transverse measure of dorsal trochlear surface; (1) approximately equal (Clarke et al., 2006: 134).
131. Ulnare: (0) "heart shaped," little differentiation into short dorsal and ventral rami; (1) V-shaped, well-developed dorsal and ventral rami (Clarke et al., 2006: 139).
132. Ulnare, ventral ramus (crus longus, Baumel and Witmer, 1993): (0) shorter than dorsal ramus (crus brevis); (1) same length as dorsal ramus; (2) longer than dorsal ramus (Clarke et al., 2006: 140).
133. Ulnare, ventral ramus, tubercle where this ramus joins the dorsal margin: (0) absent; (1) present (Clarke and Chiappe 2001: 35).
134. Semilunate carpal and metacarpals: (0) complete proximal fusion; (1) complete proximal and distal fusion (Clarke et al., 2006: 141).
135. Carpometacarpus, proximal end, ventral surface, conspicuous fossa posterodistal to pisiform process: (0) absent or shallow; (1) deep pit (Clarke and Chiappe, 2001: 47).
136. Carpometacarpus, ventral surface, infratrochlear fossa deeply excavating proximal surface of pisiform process: (0) absent; (1) present (Clarke et al., 2006: 148).
137. Carpometacarpus, proximal end, ulnocarpal articular facet: (0) absent; (1) present; (2) well projected (i.e., distal extent approaching anteroposterior width of carpal trochlea). ORDERED (Clarke and Chiappe, 2001: 38).
138. Carpometacarpus, proximal half of the element in dorsal view, posterior side of the carpal trochlea: (0) smooth or slight depression at the distal end; (1) deep groove at the distal end.
139. Carpometacarpus, distal end, metacarpals II and III, articular surfaces for digits: (0) metacarpal II subequal to or surpassing metacarpal III in distal extent; (1) metacarpal III extending farther (Clarke et al., 2006: 150).
140. Metacarpal I, anteroproximally projected muscular process: (0) tip of process just surpasses the distal articular facet for phalanx 1 in anterior extent; (1) tip of extensor process conspicuously surpasses articular facet by approximately half the width of facet, producing a pronounced knob; (2) tip of extensor process conspicuously surpasses articular facet by approximately the width of facet, producing a pronounced knob. ORDERED (Clarke et al., 2006: 144).
141. Intermetacarpal space (between metacarpals II and III): (0) reaches proximally as far as the distal

- end of metacarpal I; (1) terminates distal to end of metacarpal I (Clarke et al., 2006: 149).
142. Intermetacarpal process or tubercle: (0) present as scar; (1) present as tubercle or flange (Clarke et al., 2006: 151).
 143. Metacarpal III, proximal portion, ventral side: (0) smooth or very slight expansion; (1) distinct tuber present.
 144. Manual digit II, phalanx 2, internal index process on posterodistal edge: (0) absent; (1) present (Clarke et al., 2006: 154).
 145. Manual digit III, phalanx 1: (0) flexor process prominent (triangular); (1) flexor process small or absent (rod shaped) (Clarke 2004).
 146. Manual digit III, phalanx 1, length: (0) greater than or equal to 50% the length of digit II, phalanx 1; (1) less than 50% the length of digit II, phalanx 1.
 147. Ilium/ischium, distal coossification to completely enclose the ilioischadic fenestra: (0) absent; (1) present (Clarke et al., 2006: 156).
 148. Ilium, preacetabular portion: (0) approach on midline, open, or cartilaginous connection; (1) coossified, dorsal closure of "iliosynsacral canals" (Clarke et al., 2006: 162).
 149. Ilium, preacetabular portion, extension anterior to first sacral vertebrae: (0) no free ribs overlapped; (1) one or more ribs overlapped (Clarke et al., 2006: 163).
 150. Ilium, postacetabular blade: (0) dorsoventrally oriented; (1) mediolaterally oriented (Clarke et al., 2006: 164).
 151. Ilium, antitrochanter, posterior extent in lateral view: (0) anterior portion of articulation between the ilium and ischium visible; (1) posterior extent of the antitrochanter hides the anterior portion of ilioischadic fenestra.
 152. Ilium, relative lengths of the anterior and posterior ilia (relative to the middle of the acetabulum): (0) approximately equal in length to each other; (1) posterior portion longer than the anterior portion; (2) anterior portion longer than the posterior portion (Lee et al., 1997:20).
 153. Ilium, m. cuppedicus fossa as broad, mediolaterally oriented surface directly anteroventral to acetabulum: (0) present; (1) surface absent, insertion variably marked by a small entirely lateral fossa anterior to acetabulum (Clarke et al., 2006: 166).
 154. Pubis, preacetabular pectineal process: (0) absent; (1) present and small flange; (2) present as a well-developed flange. ORDERED (Clarke et al., 2006: 159).
 155. Ischium, dorsal surface of the posterior portion: (0) dorsal process present; (1) straight, no dorsal process (modified from Clarke et al., 2006: 157).
 156. Ischium, distal portion: (0) same width or expanded posteriorly; (1) tapers posteriorly.
 157. Femur, proximal end, posterior trochanter: (0) hypertrophied, "shelflike" conformation (in combination with development of the trochanteric shelf; see Hutchinson, 2001); (1) absent (Clarke et al., 2006: 173).
 158. Femur, posteriolateral margin of the proximal antitrochanteric articular surface (= crista trochanteris): (0) about the same proximal level as the head, rounded edge, no lip present, surface flattened to slightly convex; (1) markedly projected proximally curved sharply to form a lip that faces medially, surface highly concave (modified from Mayr and Clarke, 2003: 97).
 159. Femur, distal end, laterally projected fibular trochlea: (0) present, developed as small notch; (1) a shelflike (Clarke et al., 2006: 178).
 160. Femur, distal end, external and fibular condyles: (0) essentially equal in size and in their distal extension relative to the internal condyle; (1) greatly enlarged and project distally beyond level of internal condyle (Lee et al., 1997: 44).
 161. Femur, distal end, rotular (= patellar) groove: (0) broad and shallow; (1) narrow and deep (Lee et al., 1997: 48).
 162. Femur, distal end, popliteal fossa: (0) shallow, almost flat; (1) very deep, extending anteriorly (Lee et al., 1997: 49).
 163. Tibiotarsus, cranial cnemial crest, distal projection relative to lateral cnemial crest: (0) longer or about the same length; (1) shorter (modified from Bertelli and Chiappe, 2005: 48).
 164. Tibiotarsus, proximal surface, posterior tuber: (0) convex; (1) concave.
 165. Tibia/tarsal formed condyles: (0) medial condyle projecting further anteriorly than lateral; (1) equal in anterior projection (Clarke et al., 2006: 182).
 166. Tibia/tarsal formed condyles, extensor canal: (0) absent; (1) an emarginated groove; (2) groove bridged by an ossified supratendinal bridge. ORDERED (Clarke et al., 2006: 183).
 167. Tibiotarsus, extensor canal (groove or ossified), location: (0) between the distal condyles; (1) proximal to the medial condyle (modified from Bertelli and Chiappe, 2005: 59).
 168. Tibia/tarsal formed condyles, mediolateral widths: (0) medial condyle wider; (1) approximately equal;

- (2) lateral condyle wider. ORDERED (Clarke et al., 2006: 185).
169. Tibia/tarsal formed condyles: (0) gradual sloping medial constriction of condyles; (1) no medial tapering of either condyle (Clarke et al., 2006: 186).
170. Tibia/tarsal formed condyles, intercondylar groove: (0) mediolaterally broad, approximately 1/3 width of anterior surface; (1) less than 1/3 width of total anterior surface (Clarke et al., 2006: 187).
171. Tibiotarsus, medial condyle, length relative to lateral condyle in anterior view: (0) subequal; (1) slightly shorter; (2) much shorter (Bertelli and Chiappe, 2005: 53).
172. Tibiotarsus, distal end, medial side of the medial condyle: (0) slight depression near anterior margin; (1) deep pit in anterior margin and a groove along the posterior margin (Lee et al., 1997: 39).
173. Tarsometatarsus, projected surface or grooves on proximoposterior surface (associated with the passage of tendons of the pes flexors in Aves; hypotarsus): (0) developed as posterior projection with flat posterior surface; (1) projection, with distinct crests and grooves; (2) at least one groove enclosed by bone posteriorly. ORDERED (Clarke et al., 2006: 195).
174. Tarsometatarsus, intercotylar prominence, proximal extension relative to hypotarsus: (0) extended beyond hypotarsus; (1) level with hypotarsus (Clarke et al., 2006: 194).
175. Tarsometatarsus, digit I: (0) present; (1) absent (Lee et al., 1997: 32).
176. Tarsometatarsus, proximal vascular foramen (foramina): (0) one, between metatarsals III and IV; (1) two present (Clarke et al., 2006: 196).
177. Tarsometatarsus, distal end, plantar surface of trochlea II and IV: (0) weakly expanded; (1) expanded into distinct "wings" (Houde, 1988: 53).
178. Metatarsal II, distal plantar surface, fossa for metatarsal I (fossa metatarsi I; Baumel and Witmer, 1993): (0) absent; (1) shallow notch; (2) conspicuous ovoid fossa. ORDERED (Clarke et al., 2006: 199).
179. Metatarsal II, articular surface for first phalanx: (0) ginglymoid; (1) rounded (Clarke et al., 2006: 200).
180. Tarsometatarsus: trochlea II, distal extent of trochlea II relative to trochlea IV: (0) approximately equal in distal extent; (1) trochlea II shorter than trochlea IV, but reaching distally further than base of trochlea IV trochlea; (2) trochlea II shorter than trochlea IV, reaching distally only as far as the base of trochlea IV. ORDERED (Clarke et al., 2006: 205).
181. Distal vascular foramen: (0) simple, with one exit; (1) forked, two exits (plantar and distal) between metatarsals III and IV (Clarke et al., 2006: 203).
182. Metatarsal III, trochlea in plantar view, proximal extent of lateral and medial edges of trochlea: (0) absent, trochlear edges approximately equal in proximal extent; (1) present, lateral edge extends farther (Clarke et al., 2006: 204).

TAXON SCORES

	10	20	30	40	50	60	70
<i>Ichthyornis dispar</i>	A?0?00??0?	0?0???0???	??????????	010A?1000?	?1000000?-	0??0002000	0010A01?A1
<i>Apsaravis ukhaana</i>	??????????	??????????	??????????	??????0???	??????101?	0??11?????	????200A00
<i>Anatalavis oxfordi</i>	101?0000?0	?1????0000	100????11?1	?10?11????	???0??????	???1???100	????2110??
<i>Anas platyrhynchos</i>	1011010000	1100000101	1001111111	0101111210	0100011001	0111010100	1111211022
<i>Chauna torquata</i>	0011000000	0100000000	100B111011	0101111110	1100011001	0111010100	1100211022
<i>Gallinuloides wyomingensis</i>	101?000000	11?00000??	??????????	????11?1?	0?0???1?0?	0??10?????	????21002?
<i>Gallus gallus</i>	0011000000	1100000000	1002011111	0001111200	0100011001	0101010100	1011210222
<i>Crax pauxi</i>	1011000?00	-1100000000	1002011111	0001111200	0100011001	0101010100	1001210222
<i>Gavia immer</i>	0011010000	1111001000	100111----	0102011200	010100100?	01010100-0	0000210022
<i>Apteryx owenii</i>	1110110011	11-10--11?	0010000000	1100000200	0011101011	1--1112021	0001210012
<i>Emeus crassus</i>	1011100011	0110001-1?	0010100000	0100000200	1001110000	0101111000	0???210022
<i>Struthio camelus</i>	1111111110	0101101011	0100010000	1100000100	1001001010	1101111000	0100210020
<i>Palaeotis weigelti</i>	??1?11??1?	?1??1?101?	00102000??	?100?0????	?0?10?1?1?	1??11?20?0	0???210???

	10	20	30	40	50	60	70
<i>Rhea americana</i>	111111?1?0	0100100012	0000010000	1000000200	001100101?	1101111000	0000210012
<i>Dromaius novaehollandiae</i>	1111?0?100	0001101110	0100000000	0000000100	000100101?	1101111000	0001210022
<i>Crypturellus undulatus</i>	1110111010	1001010111	0010200000	1010000201	0011001110	1001111010	0110210122
<i>Nothura maculosa</i>	1110101010	1001011011	0010200000	1010000201	0011001110	1001111020	0100210222
<i>Eudromia elegans</i>	1110111010	1001010011	0010200000	1010000200	1011001110	1001111020	0100210222
<i>Tinamus major</i>	11101?1A10	1001010011	0010200000	1010000201	0011001110	1001111000	0100210122
<i>Lithornis</i>	1?1??1??1?	?0????????	0??0?00000	???000??0?	?001?11?1?	1?01111???	????2120B1
<i>Lithornis celetius</i> holotype	1?1011101?	1011010?1?	0110100000	1100000100	100100????	??????????	?????????1
<i>Lithornis celetius</i> postcrania	??????????	??????????	??????????	??????????	??????????	??????????	??????2?11
<i>Lithornis celetius</i> others	??????????	??????????	??????????	??????????	??????????	???111?001	0??1212???
<i>Lithornis celetius</i> combined	1?1011101?	1011010?1?	0110100000	1100000100	100100????	???111?001	0??1212?11
<i>Lithornis plebius</i>	???????0??	?0?1?1????	??1???0000	1100000100	1011001??1	11011?1???	?10?2120?1
<i>Lithornis promiscuus</i> holotype	111???????	??????????	??????????	?????0010?	?01100111?	1101111001	0101212011
<i>Lithornis promiscuus</i> skull	1110110010	1011010012	011010?000	110???????	??????????1	??????????	??????????
<i>Lithornis promiscuus</i> combined	1110110010	1011010012	011010?000	110??0010?	?011001111	1101111001	0101212011
<i>Lithornisvulturinus</i> MGUH26770	??11111?10	?0110?001?	0110100000	1000000?00	1011????1?	???111?0?1	0???21201?
<i>Paracathartes howardae</i>	111?????1?	?0????1?12	011?1?0000	1000?0000?	?011001111	1101??1001	01012?2???
<i>Pseudocrypturus cercanaxius</i>	1110111010	1011010?12	001020?00?	1?0?00?100	1011??1?11	1101111001	0???2?????
Siber and Siber	?11?111?1?	??110?01??	??????????	??????????	10????1?1?	1??11?10?1	????2120??
<i>Pseudocrypturus</i> combined	1110111010	1011010112	001020?00?	1?0?00?100	1011??1?11	1101111001	0???2120??
<i>Calciavis grandei</i> referred	111?1?101?	?0?????0??	?0????????	?????0?100	1???0?11?1	1?011110?1	????2120??
<i>Calciavis grandei</i> holotype	?11?111?1?	??11?100??	?0????????	1???0????00	1??10?1?11	1??111?0?1	?101212011
FMNH PA 739	11????????	??????????	??????????	??????????	???????1?11	1??1??1???	?????12011
FMNH PA 729 wing	??????????	??????????	??????????	??????????	??????????	??????????	??????????
WSGS U1b-2001	??????????	??????????	??????????	??????????	??????????	??????????	??????????

(0,1) = A, (1,2) = B

	80	90	100	110	120	130	140
<i>Ichthyornis dispar</i>	0011???010	1010000000	110?011101	-1100?1000	0101100110	00010?1011	1201010?00
<i>Apsaravis ukhaana</i>	000??0??00	????0??00	000?00?000	-101011?00	0?011000B1	11100?0010	0?0A000??0
<i>Anatalavis oxfordi</i>	???????100	?1?0?01000	1111011101	-01001?001	?110011200	00010011??	?2?1000002
<i>Anas platyrhynchos</i>	1000211100	3110011100	111-111111	-010000001	1010011200	0001001101	1211000002
<i>Chauna torquata</i>	1000210100	30100A1100	1111011011	-010002001	1110001200	0001001100	1211101112
<i>Gallinuloides wyomingensis</i>	???????00	?110021000	0111011111	-1101110??	?110011??0	000?011100	11?1001?02
<i>Gallus gallus</i>	0000200100	1110120010	0111011111	-100101101	1110011200	0001011100	1111001112
<i>Crax pauxi</i>	1000201100	1110020010	0111011111	-100101101	1110011200	0001011100	1111000012
<i>Gavia immer</i>	1000100000	3110011000	1110011101	-010000001	0010001200	0001001100	1101000100
<i>Apteryx owenii</i>	110?000021	00110???-1	-1----0-1-	-010010-10	--10-01--0	00010---0-	??-?-?-?---
<i>Emeus crassus</i>	???????0121	00110----1	-----	-----	-----	-----	-----
<i>Struthio camelus</i>	110-001100	10110----1	-1----1-1-	-010010020	--10-01--0	00001---0-	???10-101-
<i>Palaeotis weigelti</i>	110???1?0?	??110???-1	11???11-1-	-??0110010	-?????????	?????-???-	???11110?2
<i>Rhea americana</i>	110---0120	00010----1	-1----0-1-	-010110-20	0110--1--0	00010---0-	---1001?00
<i>Dromaius novaehollandiae</i>	110---100	1001-----1	-1----0-1-	-110000-21	0-10--1--0	0001----0-	---1--1?--
<i>Crypturellus undulatus</i>	1101001100	1?10100010	111001111-	1100101101	1110011200	0001011000	1101102012
<i>Nothura maculosa</i>	1101200100	0?10100010	111-01101-	0100101101	1110011200	0001011000	1101102012
<i>Eudromia elegans</i>	1101101100	1?10100010	111001111-	1100101101	1110011200	00010110?0	1101002012
<i>Tinamus major</i>	1101100100	0?10100010	111001111-	1100101101	1110011200	00011110?0	1101102012
<i>Lithornis</i>	?1?A??A11?	110?000?0?	1110?11101	??01??1001	??100??B10	00010?1000	11?1?1??A1
<i>Lithornis celetius</i> holotype	?00???????	???????????	???????????	???????????	???????????	???????????	???????????
<i>Lithornis celetius</i> postcrania	???????????	?????????00	11101?1101	-?020??001	10?????21?	?????????00	???111??12
<i>Lithornis celetius</i> others	???????110	000000?000	????1?????	?00201?001	10100002?0	00010010??	???????????
<i>Lithornis celetius</i> combined	?00????110	000000?000	11101?1101	-?0201?001	1010000210	0001001000	???111??12
<i>Lithornis plebius</i>	???010????	??????0000	1110111101	-002011001	1010000210	0001001000	1111111112
<i>Lithornis promiscuus</i> holotype	110020?110	1000000000	1110111101	-002111001	1010001210	0001001000	1111111112
<i>Lithornis promiscuus</i> skull	???????????	???????????	???????????	???????????	???????????	???????????	???????????
<i>Lithornis promiscuus</i> combined	110020?11?	1000000000	1110111101	-002111001	1010001210	0001001000	1111111112
<i>Lithornis vulturinus</i> MGUH26770	???????????	??????0000	11?0?1????	-002011???	??10001??0	000?00?0?0	1111????12
<i>Paracathartes howardae</i>	?10021????	??????0?00	1110111101	-00211?001	?010001210	0001001000	???11111?2

	80	90	100	110	120	130	140
<i>Pseudocrypturus cercanaxius</i>	??????????	??????????	??????????	??????????	??????????	??????????	??????????
Siber and Siber	??????0??0	1?000000?0	1?1??11?01	-0???01??? ?0?0?11?10	00010010?0	???1111??2	
<i>Pseudocrypturus</i> combined	??????0??0	1?000000?0	1?1??11?01	-0???01??? ?0?0?11?10	00010010?0	???1111??2	
<i>Calciavis grandei</i> referred	??????0?10	100000?0?0	1????111??	?002001001	101?0??11?	?0?0?01?0?	???1??1112
<i>Calciavis grandei</i> holotype	11?0200??0	10000????0	?????11???	?020?1001	???????11?	?00?01?00	1111111112
FMNH PA 739	1100?????0	10?00?????	??????????	?????01???	?????????0	00010010?0	?????????2
FMNH PA 729 wing	??????????	?????????00	?11????1??	?0????100?	?10?01???	?00??0?0?0	1??1111???
WSGS U1b-2001	??????0???	??????????	?11?0?0???	???????1???	?10011?1?	?00??0?0??	11????????

(0,1) = A, (1,2) = B

	150	160	170	180
<i>Ichthyornis dispar</i>	00010?0000	0201011010	0000110100	00A0010102 00
<i>Apsaravis ukhaana</i>	000???0000	020011?0?0	????100211	?001?00011 0?
<i>Anatalavis oxfordi</i>	100011?1?1	??????????	??????????	?????????? ??
<i>Anas platyrhynchos</i>	1000101111	1101-00100	0001020100	1020010102 10
<i>Chauna torquata</i>	1000101111	1211-11110	0021020200	1010010210 10
<i>Gallinuloides wyomingensis</i>	1010111?11	??0-110?0	0?0?0201?0	00?001?111 ??
<i>Gallus gallus</i>	1100101111	0210-01110	0011020100	0020011211 11
<i>Crax pauxi</i>	1100101111	0010-11010	0001020100	0020011210 11
<i>Gavia immer</i>	0001101010	0111-01011	0001020110	1020010102 11
<i>Apteryx owenii</i>	-----0110	1202001010	0011021100	1010011100 00
<i>Emeus crassus</i>	-----0110	0200001111	0001021100	0011010?01 ?0
<i>Struthio camelus</i>	000-100110	0102001011	1111111110	0111110--- 00
<i>Palaeotis weigelti</i>	0?0?--01?0	100???1010	0?1?11??0	?101?0010 ??
<i>Rhea americana</i>	00?---1100	110?101011	1101011100	2111110000 00
<i>Dromaius novaehollandiae</i>	--?---0110	?10?101011	0101111100	1111110000 00
<i>Crypturellus undulatus</i>	1000010011	0202001110	0001021100	2010011111 10
<i>Nothura maculosa</i>	1000010011	0202001110	0001021100	1010011111 11
<i>Eudromia elegans</i>	1000010011	1202001110	0011021100	1010011111 11
<i>Tinamus major</i>	1000010011	1002001110	0001021100	2010011111 11
<i>Lithornis</i>	00?0??A001	?0?0?1?1?	???010000	?1?1111A 10

	150	160	170	180	
<i>Lithornis celetius</i> holotype	1????00?1	?202??10??	??????????	??????????	??
<i>Lithornis celetius</i> postcrania	101???????	??????????	?????11???	??????1?11	10
<i>Lithornis celetius</i> others	???????0??	?????????10	00????????	??10?11?11	10
<i>Lithornis celetius</i> combined	101???00?1	?202??1010	00???11???	??10?11?11	10
<i>Lithornis plebius</i>	1010??00?1	0?01011010	0001011100	1010011111	11
<i>Lithornis promiscuus</i> holotype	101???0011	12010?1010	0001011100	1010011111	11
<i>Lithornis promiscuus</i> skull	??????????	??????????	??????????	??????????	??
<i>Lithornis promiscuus</i> combined	101???0011	12010?1010	0001011100	1010011111	11
<i>Lithornis vulturinus</i> MGUH26770	1??0110011	0201??0??	??????????	??????????	??
<i>Paracathartes howardae</i>	100???????	??????1010	0001011100	1010011111	11
<i>Pseudocrypturus cercanaxius</i>	??????????	??????????	??????????	??????????	??
Siber and Siber	???001????	???????010	?0??11100	10?001?1?0	??
<i>Pseudocrypturus</i> combined	???001????	???????010	?0??11100	10?001?1?0	??
<i>Calciavis grandei</i> referred	10??01????	??????????	??????????	???00?111?	??
<i>Calciavis grandei</i> holotype	1010010?11	?201101010	0001?????0	??1?011110	?0
FMNH PA 739	10?0010?11	0201?010?0	0???011?0?	?0100?1110	??
FMNH PA 729 wing	101001????	??????????	??????????	??????????	??
WSGS U1b-2001	1?????????	??????????	?????11100	1??001?110	??

(0,1) = A (1,2) = B

APPENDIX 2

LITHORNITHID TERMINAL TAXA

Lithornis celetius Houde, 1988 (fig. 34)

AGE: Late Paleocene (earliest Tiffanian = T1) (Lofgren et al., 2004).

OCCURRENCE: Bangtail Quarry, Fort Union Formation, western Crazy Mountain Basin, Park County, Montana.

HOLOTYPE: USNM 290601, partial skull, quadrates, fragmentary pelvis, right femur lacking distal end, radiales, a single caudal vertebra.

POSSIBLY REFERABLE MATERIAL: USNM 290554, right coracoid, left scapula, left carpo-metacarpus, distal end of the right tarsometatarsus, fragments; USNM 336200, right quadrate, distal end of the right radius; PU 16961, much of the mandible, presacral vertebrae, partial furcula, nearly complete sternum, parts of the radius, incomplete left femur, incomplete tarsometatarsi, pedal elements; PU 23483; partial right mandibular ramus, partially articulated cervical vertebrae, fragments of other vertebrae, fragment of the coracoid, proximal end of left humerus; PU 23484, right scapula, right humerus, portion of an ulna, phalanx II-1, distal portion of a right tarsometatarsus; PU 23485, complete right humerus, anterior portion of a left ilium.

REVISED DIAGNOSIS: The holotype of *Lithornis celetius* is unique among Aves with the following combination of characters: ventral pterygoid fossa (C23:1); lateral exposure of the ventral process of the lacrimal broad (C13:1); quadrate without a small fossa on the posterior portion of the body (C38:0); wide preorbital region; extensive contact between the lateral ectethmoid and the lacrimal (C16:1); and the largest pectineal process of the pubis among lithornithids (C154:2). The holotype of *Lithornis celetius* differs from *Pseudocrypturus cercanaxius* (USNM 336103) and a referred specimen of *Lithornis promiscuus* (USNM 391983) in having much more laterally expanded preorbital region (dorsal portion of the lacrimal). *Lithornis celetius* differs from the holotype of *Lithornis promiscuus* (USNM 336535), *Lithornis plebius* (USNM

336534), and *Paracathartes howardae* (USNM 424067) by the absence of small foramina or fossae on the posterior side of the otic process of the quadrate (C38:0). *Lithornis celetius* differs from *Calciavis grandei* (AMNH 30578) by the presence of a more developed preacetabular pectineal process of the pubis.

The referred specimens of *Lithornis celetius* differs from *Lithornis vulturinus* (NHMUK A 5204) in its humerus with a less arcuate pectoral crest and sternum with short sternocoracoidal process and more parallel margins. *Lithornis celetius* differs from all other lithornithids in the presence a deep groove on the proximal portion of the coracoid and the presence of at least 13 synsacral vertebrae.

REMARKS: *Lithornis celetius* is the oldest confirmed lithornithid to date. Houde (1988) reported that *Lithornis celetius* is essentially represented by the entire skeleton and assigned all lithornithidlike specimens from the Bangtail Quarry (and Polecat Bench specimens) to the taxon. Even though all the specimens from the quarry are similar in size and appear to belong to a lithornithid, the partial skeletons have few overlapping elements and, of those overlapping elements, most of the shared features are plesiomorphic for Aves. To make matters more complicated, the avian material from the Bangtail Quarry was collected over decades by different institutions (Houde, 1988), and thus the association of the different partial skeletons and the number of individuals is unknown. Therefore, we take a conservative approach and restrict the diagnosis (see above) to the holotype consisting of a partial skull without the mandible and fragmentary bones of the postcranium. All other material from the type locality is included in the second part of the diagnosis. We scored the holotype skeleton of *Lithornis celetius* as a separate terminal taxon from the referred material in the phylogenetic analysis. We also included a combined *Lithornis celetius* terminal taxon that includes the scores from the holotype and all the referred material from Bangtail Quarry. The specimens from the Polecat Bench Formation

(e.g., PU 20510) in Wyoming cannot be confidently assigned to *Lithornis celestius* because all the character states shared with *Lithornis celestius* are not exclusive to that taxon.

KEY REFERENCES: Houde, 1988.

Lithornis promiscuus Houde, 1988 (figs. 33, 34)

AGE: Late Paleocene (middle Clarkforkian North American land mammal age (NALMA) = Cf2) (Lofgren et al., 2004).

OCCURRENCE: *Plesiadapis cookei* zone Willwood Formation, Clarke's Fork Basin, Park County, Wyoming.

HOLOTYPE: USNM 336535, fragmentary, disarticulated skull including the premaxillae, quadrates, and mandible, coracoids, scapulae, sternum, furcula, humeri, ulnae, ulnares, left radiale, carpometacarpus, much of the presacral column, synsacrum, anterior caudal vertebrae, pygostyle, nearly complete pelvis, partial femora, tibiotarsi, tarsometatarsi, and other fragments.

POSSIBLY REFERABLE MATERIAL: USNM 391983, complete skull (fig. 33); AMNH 21901, poorly preserved and crushed skull and mandible; possibly AMNH 21900, partial synsacrum.

REVISED DIAGNOSIS: *Lithornis promiscuus* is unique among Aves with the following combination of characters: quadrate with a small fossa on the posterior portion of the body (C38:1); pair of distinct furrows anterior to the external naris of the premaxilla (C2:1) and of the dentary (C49:1); acromion of the scapula with laterally hooked tip with small foramina on the posterior side (C104:2); glenoid of the scapula large and occupies nearly 50% of the width of the shaft of the scapula; small foramina ventral to the acrocoracoid process on the medial side of the coracoid (C95:1); narrow intermetacarpal space; conspicuous deep pit posterodistal to pisiform process on the ventral surface of the proximal end of the carpometacarpus (C135:1); distinct tuber present on the ventral side of the proximal portion of metacarpal III (C143:1); and distal end of the ischium blunt and with slight dorsal expansion.

Lithornis promiscuus differs from *Lithornis celestius* by the presence of small foramina or fossae on the posterior side of the otic process of the quadrate and from *Lithornis plebius* by the absence of a pointed, ventrally directed process of the pygostyle. *Lithornis promiscuus* differs from *Calciavis grandei* (AMNH 30578) by the presence of a dorsal process on the dorsal margin of the ischium.

The referred skull of *Lithornis promiscuus* (USNM 391983) differs from *Pseudocrypturus cercanaxius* (USNM 336103) by the presence of posterolateral portion of the nasal that is rounded and not medioventrally thin in lateral exposure.

REMARKS: The holotype of *Lithornis promiscuus* (USNM 336535) is well preserved and represents much of the skeleton, save the skull, of one individual. Fortunately, the skull fragments preserved, quadrates, premaxilla, and mandible fragments, are diagnostic for lithornithids and basal avians. The nearly complete referred skull agrees with the all aspects of the morphology of holotype, but it is unclear whether it is unambiguously assignable to *Lithornis promiscuus* given that all the synapomorphies shared between the skull and the holotype are found in other lithornithids (e.g., *Pseudocrypturus cercanaxius*). Therefore, the skull is scored separately into the phylogenetic analysis and combined in a composite *Lithornis promiscuus* terminal taxon including the skull and the holotype.

Lithornis promiscuus is found at the same localities as *Lithornis plebius* (Houde, 1988). Even though the two species are similar in morphology, we support the decision by Houde (1988) to separate the taxa because: (1) *Lithornis plebius* is 75% the size of *Lithornis promiscuus*; (2) the distal end of the ischium is blunt in *Lithornis promiscuus* whereas it is tapered in *Lithornis plebius*; (3) the ventral process of the pygostyle is blunt in *Lithornis promiscuus* whereas it is tapered in *Lithornis plebius*; and (4) the antitrochanter of *Lithornis plebius* does not extend past the anterior extension of the articulation between the ischium and ilium in lateral view where it does in *Lithornis promiscuus*.

KEY REFERENCES: Houde, 1988.

Lithornis plebius Houde, 1988

AGE: late Paleocene (Clarkforkian 2 NALMA = Cf2) (Lofgren et al., 2004).

OCCURRENCE: *Plesiadapis cookei* zone Willwood Formation, Clark's Fork Basin, Park County, Wyoming.

HOLOTYPE: USNM 336534, posterior portion of the skull, quadrates, dentary, partial furcula, coracoids, scapulae, right humerus, ulnae, fragments of the radii, ulnare, carpometacarpi, parts of the presacral column, partial synsacrum, pygostyle, partial pelvis, femora, tibiotarsi, fibulae, left tarsometatarsus, and other fragments.

REFERRED MATERIAL: AMNH 21902; thoracic vertebrae, right distal portion of the tarsometatarsus, radii, left carpometacarpus, proximal portion of the femur; AMNH 21903; parts of the radii, proximal and distal portions of the right and nearly complete left carpometacarpus proximal and distal portions of the tarsometatarsus, left coracoid, right scapula, much of the ulna, much of the right femur, proximal half of the tarsometatarsus, proximal and distal portions of the left and right humerus, vertebral fragments, sacrum, pedal elements, skull roof.

REVISED DIAGNOSIS: *Lithornis plebius* is unique among Aves with the following combination of characters: quadrate with small fossae on the posterior side of the body (C38:1); the absence of small foramina or fossae on the posterior side of the otic process of the quadrate (C43:0); pair of distinct furrows on the anterior portion of the dentary (C49:1); foramina present on the posteroventral surface of the hooked acrocoracoid process of the coracoid (C95:1); acromion of the scapula with laterally hooked tip with small foramina on the posterior side (C104:2); narrow intermetacarpal space; conspicuous deep pit posterodistal to pisiform process on the ventral surface of the proximal end of the carpometacarpus (C135:1); distinct tuber present on the ventral side of the proximal portion of metacarpal III (C143:1); distal end of the ischium tapered and with slight dorsal expansion; and extra projection on the anterior cnemial crest observed in medial view.

Lithornis plebius differs from *Lithornis promiscuus* and *Calciavis grandei* (AMNH 30578) by the presence of a distally tapering ischium. *Lithornis plebius* differs from *Lithornis celestius* by the presence of a smaller pectineal process of the pubis. The skull of *Lithornis plebius* is estimated to be much smaller than that of *Pseudocrypturus cercanaxius* (USNM 336103).

REMARKS: *Lithornis plebius* is one of the smallest lithornithids known (Houde, 1988). The well-preserved skeleton is from a single individual and almost every element is represented by at least one side. The holotype was found among the remains of *Lithornis promiscuus* but is morphologically distinct (see above). A partially skeleton from Isle of Sheppey in England (NHMUK A 5503) was assigned to *Lithornis plebius* based on similarities in size and morphology. However, the holotype and NHMUK A 5503 share no unique character states and, therefore, the remains of *Lithornis plebius* are known only from Wyoming.

KEY REFERENCES: Houde, 1988.

Pseudocrypturus cercanaxius Houde, 1988

AGE: Early Eocene, 51.66 ± 0.09 Ma (Smith et al., 2008).

OCCURRENCE: Thompson Ranch, locality H, occurs in F-2 facies of Fossil Lake deposits (of Grande and Buchheim, 1994) of the Green River Formation, near Kemmerer, Wyoming.

HOLOTYPE: USNM 336103, complete skull (fig. 32) and articulated cervical vertebrae.

REFERRED MATERIAL: USNM 424078, cast of a nearly complete, articulated skeleton of the privately held Siber and Siber specimen of Houde (1988).

REVISED DIAGNOSIS: *Pseudocrypturus cercanaxius* differs from all other Aves with the following combination of characters: quadrate with a small fossa on the posterior portion of the body (C38:1); the presence of small foramina or fossae on the posterior side of the otic process of the quadrate (C43:1); pair of distinct furrows on the anterior portion of the dentary and premaxillae (C2:1); lateral exposure of the

ventral process of the lacrimal broad (C13:1); dorsoventrally compressed posterolateral portion of the nasal (C7:1); posterolaterally directed processes of the palatine (C25:2); ventral fossa of the pterygoid (C23:1); dentary strongly forked (C55:1); fingerlike process just posterior to the glenoid of the mandible (C60:1); vomer-premaxilla contact (C26:1).

Pseudocrypturus cercanaxius differs from *Lithornis celetius* by the presence of small foramina on the posterior side of the otic process of the quadrate. *Pseudocrypturus cercanaxius* differs from the referred specimens of *Paracathartes howardae* by the presence of a small foramina on the posterior side of the otic process of the quadrate (C43:1) and differs from the referred skull of *Lithornis promiscuus* (USNM 391983) by the presence of posterolateral portion of the nasal that is medioventrally thin in lateral exposure. *Pseudocrypturus cercanaxius* differs from *Calciavis grandei* (AMNH 30578) by the presence of a proportionally shorter optic process of the quadrate and overall larger size.

The referred skeleton of *Pseudocrypturus cercanaxius* (USNM 424078) differs from *Calciavis grandei* (AMNH 30578) in the greater length of the skull than the humerus, the proportionally wider shaft of the coracoid, and the slightly concave posterior margin of the sternum.

REMARKS: The holotype of *Pseudocrypturus cercanaxius* is represented by a complete skull that has been prepared on both sides, exposing details of the basicranium and palate. *Pseudocrypturus cercanaxius* was named based on its morphological similarity to extant tinamous especially in regard to the palate. A second specimen of a lithornithid (USNM 424078) from the Green River Formation was assigned to *Pseudocrypturus cercanaxius*, but the referral was not explicitly explained in Houde (1988). The holotype and referred specimen skulls are the same size and share an identical morphology (see discussion). The referred material from Europe cannot be unambiguously assigned to *Pseudocrypturus cercanaxius*.

KEY REFERENCES: Houde and Olson, 1981; Houde, 1988.

Paracathartes howardae Harrison, 1979

AGE: Early Eocene (middle Wasatchian NALMA).

OCCURRENCE: northernmost branch of Elk Creek, southwest of Basin, Wyoming and Willwood Formation, Bighorn Basin, Wyoming.

HOLOTYPE: ROM 22658, distal end of a left tibiotarsus.

REFERRED MATERIAL: All the referred material derived from a single locality representing from at least five individuals preserved together; USNM 361402-361446, 391984, 404747-404806; USNM 361415; partial skull.

REVISED DIAGNOSIS: All the diagnostic features derive from the referred specimens and not from the holotype (see below). *Paracathartes howardae* differs from all other Aves with the following combination of characters: absence of a quadrate with a small fossa on the posterior portion of the body (C38:0); the presence of small foramina or fossae on the posterior side of the otic process of the quadrate (C43:1); pair of distinct furrows on the anterior portion of the dentary and premaxillae (C49:1 and C2:1, respectively); posterolaterally directed processes of the palatine absent (C25:1); ventral fossa of the pterygoid (C23:1); fingerlike process just posterior to the glenoid of the mandible (C60:1); stout, highly curved scapula; ossified supratendinal bridge absent (C166:1); pygostyle with a foramen through the ventral portion; and asymmetrical distal end of the tarsometatarsus (C180:1).

Paracathartes howardae differs from *Lithornis plebius*, *Lithornis promiscuus*, and *Lithornis celetius* by the presence of a distally expanded scapula blade that is highly arched, the absence of a tuber on the ventral surface of the proximal portion of metacarpal III, a flattened medial edge of the acrocoracoid process, a distinct anteriorly curved acromion of the scapula, and a more proximally expanded and pointed crista tibiofibularis of the femur. *Paracathartes howardae* differs from *P. cercanaxius* by a much more medially expanded portion of the medial side of the pterygoid and the absence of posterolateral processes of the palatine,

and from *Calciavis grandei* (AMNH 30578) by the broader scapula blade and the asymmetrical distal end of the tarsometatarsus.

REMARKS: *Paracathartes howardae* was named for the distal end of a tibiotarsus and assigned to the oldest cathartid vulture by Harrison (1979). Two character states, the absence of an ossified supratendinal bridge and the medial location of the tendinal groove, led Houde (1988) to assign *Paracathartes howardae* to Lithornithiformes. However, these two character states are plesiomorphic for Aves in many analyses (Clarke, 2004) and found in a variety of basal Aves (e.g., lithornithids, tinamous) and taxa just outside Aves (e.g., *Ichthyornis dispar*) (Clarke, 2004). Other than similar size, we have not found any unambiguous apomorphies linking the holotype of *Paracathartes howardae* to the referred specimens assigned by Houde (1988). Therefore, we score only the referred material from a calcareous nodule from the Willwood Formation as described by Houde (1988).

KEY REFERENCES: Harrison, 1979; Houde, 1988.

MGUH 26770 *Lithornis vulturinus*

AGE: Lowermost Eocene, two volcanic ash layers within the Fur Formation dated to 54.5

and 54.0 Ma (Chambers et al., 2003).

OCCURRENCE: Fur Formation of Denmark.

REFERRED MATERIAL: MGUH 26770, articulated skeleton consisting of a complete skull, presacral column, left wing, and pelvis.

REMARKS: Leonard et al. (2005) assigned a nearly complete articulated skeleton of a lithornithid from the Fur Formation to *Lithornis vulturinus*, the type species of *Lithornis*. In a later paper, Bourdon and Lindow (2015) followed this assignment and rediagnosed *Lithornis vulturinus*. Their assignment of MGUH 26770 to *Lithornis vulturinus* is based only on “consistent morphology” and not a combination of character states or autapomorphies. We do not dispute their assignment, but given that there seem to be a diversity of lithornithids, this assignment is presently based on weak evidence and it likely will always be based on the fragmentary neotype (NHMUK A5204). From our observations, MGUH 26770 is unique among lithornithids based on the following characters: hooked medial processes of the pterygoids, rodlike phalanx III-1, and a larger maxillopalatine pocket formed just anterior to the ventral portion of the lacrimal.

KEY REFERENCES: Owen, 1841; Leonard et al., 2005; Bourdon and Lindow, 2015.

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ON THE COVER: A GREEN RIVER FORMATION LITHORNITHID (*CALXAVIS GRANDEI*) STANDING BY THE SHORES OF THE EOCENE FOSSIL LAKE (~ 50 MA) WITH A SMALL RALLID IN THE BACKGROUND. ART BY VELIZAR SIMEONOVSKI.